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VOL. 14, SEC. C. DECEMBER, 1936 NUMBER 12

A STRAIN OF THE VIRUS WHICH CAUSES STREAK IN TOMATO[1]

BY G. H. BERKELEY[2]

Abstract

In this paper the symptoms of a strain of tomato streak virus 1 found in Ontario are described and are compared with those produced by tomato streak virus 1 and tobacco virus 1 on the same hosts. On tobacco, variety White Burley, Adcock, etc., the Ontario strain produces necrotic local lesions on rubbed leaves followed by systemic mottling, whereas tomato streak virus 1 generally produces necrotic local lesions only, though sometimes systemic necrosis may follow. Also, on *Nicotiana sylvestris* the Ontario strain gives rise to systemic mottling with necrosis following the primary necrotic local lesions, whereas tomato streak virus 1 produces primary necrotic local lesions with or without systemic necrosis. The fact that all varieties of tobacco do not react in a similar manner to either tomato streak virus 1 or the Ontario strain is shown by a comparison of symptoms on Harrow Velvet (systemic mottling only), and White Burley or Kelley's (necrotic local lesions sometimes followed by systemic necrosis). On the other hand, all varieties tested responded to inoculation with tobacco virus 1 (tomato mosaic) by production of systemic mottling with some distortion. A series of inoculations on seven varieties of tobacco grown in the field has shown that *N. tabacum*, varieties Adcock, Gold Tip, White Burley and Greenwood, were killed within two weeks after inoculation with tomato streak virus 1, whereas the Ontario strain on the same varieties caused stunting with systemic mottling of leaf tissue, but did not kill the plants. Tests as to reaction to aging and heat have demonstrated that tomato streak virus 1, the Ontario strain of this virus, and tobacco virus 1, have similar properties in that each is viable after six months aging and each is rendered inactive after ten minutes at 90° C. Immunity tests show that tobacco virus 1 immunizes plants against infection with either tomato streak virus 1 or the Ontario strain of this virus. It is suggested, therefore, that tomato streak virus 1 and the Ontario strain of the virus may be strains of tobacco virus 1.

Introduction

Ainsworth, Berkeley and Caldwell (1) have compared tomato viruses as they occur in England and in Canada, and found that tomato streak in both countries was for the most part caused by a single virus which they called tomato streak virus 1, though mixed virus streak also occurred. In most cases where streak was caused by a mixture of viruses they found that one of the viruses concerned was tomato streak virus 1, while the other was a potato virus of the X type. A single case of stem-necrosis streak (Johnson's tobacco virus no. 9) was also encountered in the Canadian material.

Recently Smith (7) has pointed out that tomato streak virus 1 in nature may not always be a pure strain but may consist of two or more closely similar strains. In this respect tomato streak virus 1 is similar to wheat mosaic (4), tobacco mosaic (2), cucumber mosaic (5) and potato X (6, 8) viruses, each of which has been demonstrated to be made up of closely related strains.

[1] *Manuscript received October 7, 1936.*
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The purpose of the present paper is to describe the symptoms produced by a strain of tomato streak virus 1 found in Ontario, and to compare them with the symptoms produced by tobacco virus 1 and tomato streak virus 1 on the same hosts.

Material and Methods

In June, 1934, a collection of leaves from tomato plants affected with either mosaic or streak was made, and the several viruses obtained therefrom were transferred to *Nicotiana tabacum* (tobacco, 19 varieties), *Lycopersicon esculentum* (tomato, Grand Rapids), *N. glutinosa*, *N. glauca*, petunia, *Fagopyrum esculentum* (buckwheat), *Zinnia elegans* (zinnia), *N. Langsdorfii*, *N. sylvestris* and *N. paniculata*.

Tomato streak virus 1, which was described by Ainsworth, Berkeley and Caldwell (1) as being the cause of single virus streak in both England and Canada, was obtained in Ontario from tomatoes growing under glass and from tobacco growing in the field. A sample of this virus was also received from England through the kindness of G. C. Ainsworth of the Cheshunt Experiment Station. A strain of this virus was also obtained in Ontario from greenhouse tomato and field tobacco. Tobacco virus 1 was obtained from greenhouse and field tomatoes and from field tobacco.

Experimental Results

Symptoms

The results of a large number of symptomatological studies extending over a two-year period are given in Table 1.

It is of particular interest and value to note that tomato streak virus 1 does not produce the same symptom picture on all varieties of *N. tabacum*. On some varieties the symptomatology comprises primary local necrotic lesions with or without secondary systemic necrosis and stunting, whereas in other varieties the primary symptom takes the form of yellow areas followed in a few days by secondary systemic mottling with no necrosis. In the light of these results the necessity of recording the variety of *N. tabacum* used in all experimental tests is obvious.

Tomato streak virus 1 (Ontario strain) produces symptoms identical to those of tomato streak virus 1 on *N. tabacum* varieties Standup Resistant, Halley's and Harrow Velvet, but on *N. tabacum* varieties White Burley, Kelley's, Little Orinoco and Greenwood the primary local necrotic lesions are followed by systemic mottling with distortion instead of systemic necrosis. On *N. sylvestris*, tomato streak virus 1 (Ontario strain) produces local necrotic lesions followed by systemic mottling, the mottled leaves in turn becoming necrotic, whereas tomato streak virus 1 gives rise to local necrotic lesions followed sometimes by systemic necrosis.

Recently Smith (7) has described a green and a yellow strain of tomato streak that differ from the original tomato streak virus 1 and from the strain described in this paper. The green strain as a rule produces on *N. tabacum* (White Burley) no local lesions on inoculated leaves, but when it does, the

TABLE I

COMPARISON OF SYMPTOMS PRODUCED BY TOMATO STREAK VIRUS 1, TOMATO STREAK VIRUS 1 (ONTARIO STRAIN), AND TOBACCO VIRUS 1

Host	Viruses		
	Tomato streak virus 1	Tomato streak virus 1 (Ont. strain)	Tobacco virus 1
N. tabacum, varieties:—			
Standup Resistant, Halley's, Harrow Velvet	Primary yellow lesions + systemic mottling and distortion.	Primary yellow lesions + systemic mottling and distortion.	Primary yellow lesions + systemic mottling and distortion.
White Burley, Kelley's, Little Orinoco, Greenwood, Adcock	Necrotic local lesions ± systemic necrosis.	Necrotic local lesions + systemic mottling and distortion.	Primary yellow lesions + systemic mottling and distortion.
N. glutinosa	Necrotic local lesions.	Necrotic local lesions.	Necrotic local lesions.
N. Langsdorfii	Necrotic local lesions ± systemic necrosis.	Necrotic local lesions ± systemic necrosis.	Necrotic local lesions ± systemic necrosis.
N. sylvestris	Necrotic local lesions ± systemic necrosis.	Necrotic local lesions + systemic mottling with slight necrosis.	Primary yellow lesions + systemic mottling and distortion.
N. paniculata	Primary yellow lesions + systemic mottling and distortion.	Primary yellow lesions + systemic mottling and distortion.	Primary yellow lesions + systemic mottling and distortion.
N. glauca	Distinct systemic mottling of circular spot type.	Distinct systemic mottling of circular spot type.	Indistinct systemic mottling on lower leaves only.
Zinnia elegans	Primary yellow lesions.	Primary yellow lesions.	Primary yellow lesions ± systemic mottling.
Fagopyrum esculentum	Necrotic local lesions (white).	Necrotic local lesions (white).	Systemic mottling.
Petunia	Necrotic local lesions ± systemic necrosis.	Necrotic local lesions ± systemic necrosis.	Systemic mottling.
Tomato (Grand Rapids)	Necrotic lesions on stem, leaves and fruit; mottle and stunting of plant. Under certain conditions the disease may be manifest as a mottle only.	Same as for tomato streak virus 1.	Dark green to light green mottle with leaf distortion but no necrosis.

lesions are followed by severe necrosis. The yellow variant of this strain produces yellow spots on the rubbed leaves. On the other hand the Ontario strain always produces necrotic local lesions on rubbed leaves, followed by systemic mottling. On petunia the Ontario strain produces necrotic local lesions sometimes followed by systemic necrosis, whereas the strains reported by Smith give rise to systemic mottling only.

Whereas the original tomato streak virus 1 and the Ontario strain of this virus described in this paper produced necrotic local lesions on certain varieties of *N. tabacum* (varieties White Burley, Kelley's, Little Orinoco, Greenwood, and Adcock), petunia and *N. sylvestris*, tobacco virus 1 produced no necrotic local lesions on any variety of *N. tabacum*, petunia or *N. sylvestris*, but instead produced systemic mottling with some distortion.

From the above description it is apparent that the three viruses can be readily separated from each other by their reactions on *N. sylvestris*, petunia, and certain varieties of *N. tabacum*.

Table II summarizes the more important differences between tomato streak virus 1, tomato streak virus 1 (Ontario strain) and tobacco virus 1.

TABLE II

DIFFERENTIATION OF THE THREE TOMATO VIRUSES

	Virus of		
	Single virus streak	Single virus streak (Ontario strain)	Tomato mosaic (Common tobacco mosaic)
Local necrotic lesions ± systemic necrosis on *N. tabacum*, varieties White Burley, L. Orinoco, Greenwood, Kelley's and Adcock; and *N. sylvestris;* and petunia.	+	−	−
Local necrotic lesions + systemic mottling on *N. tabacum*, varieties White Burley, L. Orinoco, Greenwood, Kelley's and Adcock; and *N. sylvestris* same but with necrosis following systemic mottling; on petunia local necrotic lesions ± systemic necrosis, but no mottling.	−	+	−
Dark green to light green mottle ± distortion on *N. tabacum*, varieties White Burley, L. Orinoco, Greenwood, Kelley's and Adcock; and *N. sylvestris;* and petunia.	−	−	+

Inoculations under Field Conditions

During the summers of 1935 and 1936 a series of inoculations was made on seven varieties of *N. tabacum* growing outdoors, with the original tomato streak virus 1, tomato streak virus 1 (Ontario strain), and tobacco virus 1. The inoculations were made two weeks after the plants had been transplanted into the field, when they were about eight inches high. Very striking results were obtained in that several varieties were killed by tomato streak virus 1, whereas tomato streak virus 1 (Ontario strain) produced local necrotic lesions followed by systemic mottling and stunting of plants. Tobacco virus 1 produced only systemic mottling and stunting on all varieties.

TABLE III

DESCRIPTION OF SYMPTOMS ON *N. tabacum* OUTDOORS

Host, *N. tabacum* variety	Type	Tomato streak virus 1	Tomato streak virus 1 (Ontario strain)	Tobacco mosaic virus 1
Adcock Gold Tip W. Burley Greenwood	FC* FC B DTT	Necrotic local lesions + systemic necrosis followed by death of plant within 20 days.	Necrotic local lesions + systemic mottling. Plants not killed.	Primary yellow lesions + systemic mottling.
H. Velvet Halley's Standup Resistant	B B B	Primary yellow lesions + systemic mottling.	As in tomato streak virus 1.	As in tomato streak virus 1.

* FC = *Flue cured;* B = *Burley;* DTT = *Dark tobacco type.*

The fact that tomato streak virus 1 killed several varieties of tobacco within 20 days after they had been inoculated, while the Ontario strain of this virus produced on the same varieties only necrotic local lesions and systemic mottling with stunting, points out a still further difference between these two viruses, (Plate III, Figs. 1, 2 and 3).

Properties of the Viruses

It is interesting to note that tomato streak virus 1 and the Ontario strain of this virus have properties similar to tobacco virus 1. This would indicate that tomato streak virus 1 is closely related to tobacco virus 1, even though certain host reactions may be dissimilar. See Table IV.

TABLE IV

PROPERTIES OF THE VIRUSES

	Aging: viable after 6 months	Resistance to heat: Not viable after 10 min. at 90° C. but viable at 80° C.
Tomato streak virus 1	+	+
Tomato streak virus 1 (Ontario strain)	+	+
Tobacco virus 1	+	+

Immunity Tests

It is now generally accepted that systemic infection of a plant with a virus precludes the entrance into that plant of another strain of the same, or a very closely related virus. Therefore, if immunity of this type can be demonstrated it follows that the viruses concerned are very closely related, if not strains of the same virus. Hence, tests were made to ascertain whether or not tobacco virus 1 would establish immunity in a plant against a later inoculation with either tomato streak virus 1 or the Ontario strain of this virus.

These tests demonstrated that when plants of *N. tabacum*, variety Adcock, were inoculated with tobacco virus 1 alone, systemic infection resulted, and when these systemically infected plants were later inoculated with either tomato streak virus 1 or the Ontario strain of this virus, no further symptoms developed, indicating that immunity had been established, since the check plants (inoculated with streak virus alone) produced necrotic local lesions on the rubbed leaves, as was to be expected.

These results indicate a very close relationship between the three viruses under discussion.

Discussion

Evidence is given which demonstrates that all varieties of tobacco do not necessarily respond in a similar manner to a given virus. In so far as tobacco virus 1 is concerned, all varieties have responded in a like manner, that is, by the production of primary yellow lesions followed by systemic mottling. However, although tomato streak virus 1 produces similar symptoms in some varieties of *N. tabacum*, in others, namely Kelley's, Little Orinoco, Greenwood, Adcock and White Burley, it produces local necrotic lesions with or without systemic necrosis, while in the case of tomato streak virus 1 (Ontario strain), the same varieties react by producing local necrotic lesions followed by systemic mottling.

It would appear that the Ontario strain of tomato streak virus 1 is intermediate in its reactions between tomato streak virus 1 on the one hand, and tobacco virus 1 on the other, since on *N. tabacum* (variety Greenwood, Kelley's, Adcock, White Burley and Little Orinoco) and *N. sylvestris* necrotic local lesions are followed by systemic mottling, whereas no such systemic mottling is general with tomato streak virus 1, and systemic mottling only occurs with tobacco virus 1.

The fact that these two streak viruses have properties (aging and resistance to heat) similar to those of tobacco virus 1, and the further fact that tobacco virus 1 is capable of immunizing plants against either of these streak viruses would indicate that tomato streak virus 1, and the Ontario strain of this virus may be strains of tobacco virus 1.

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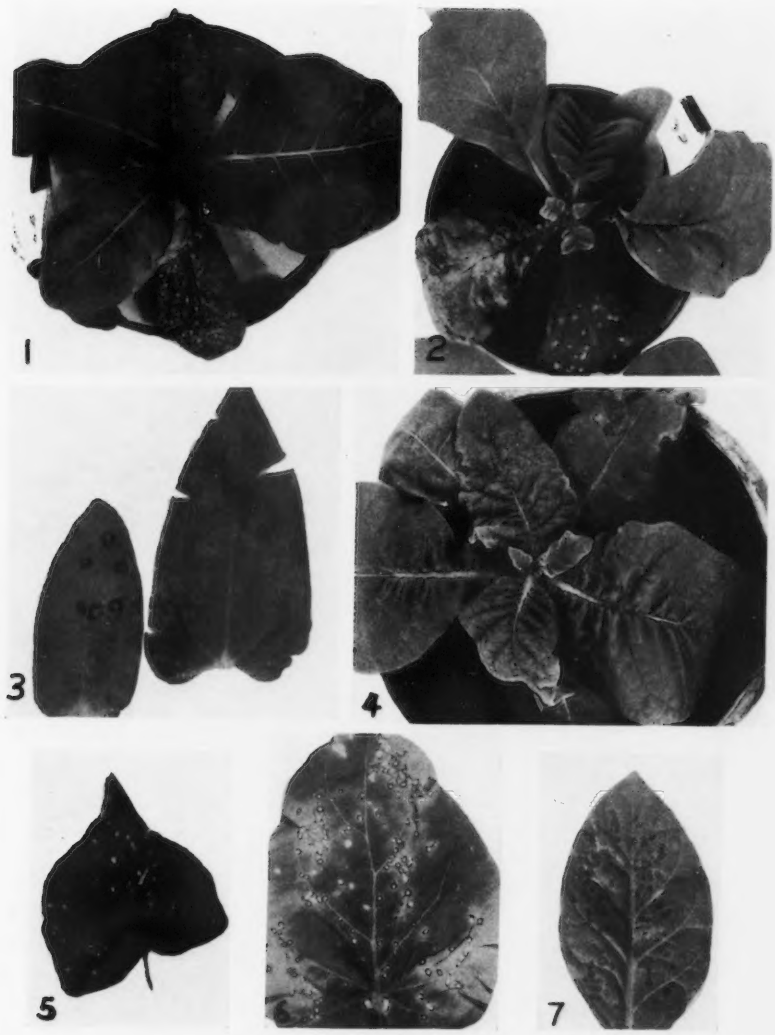
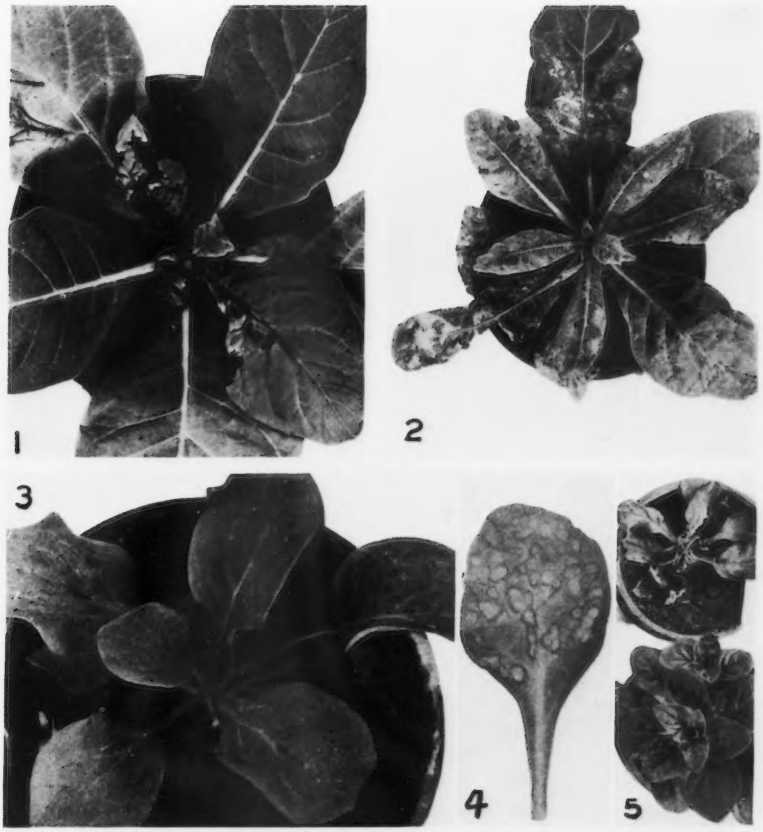
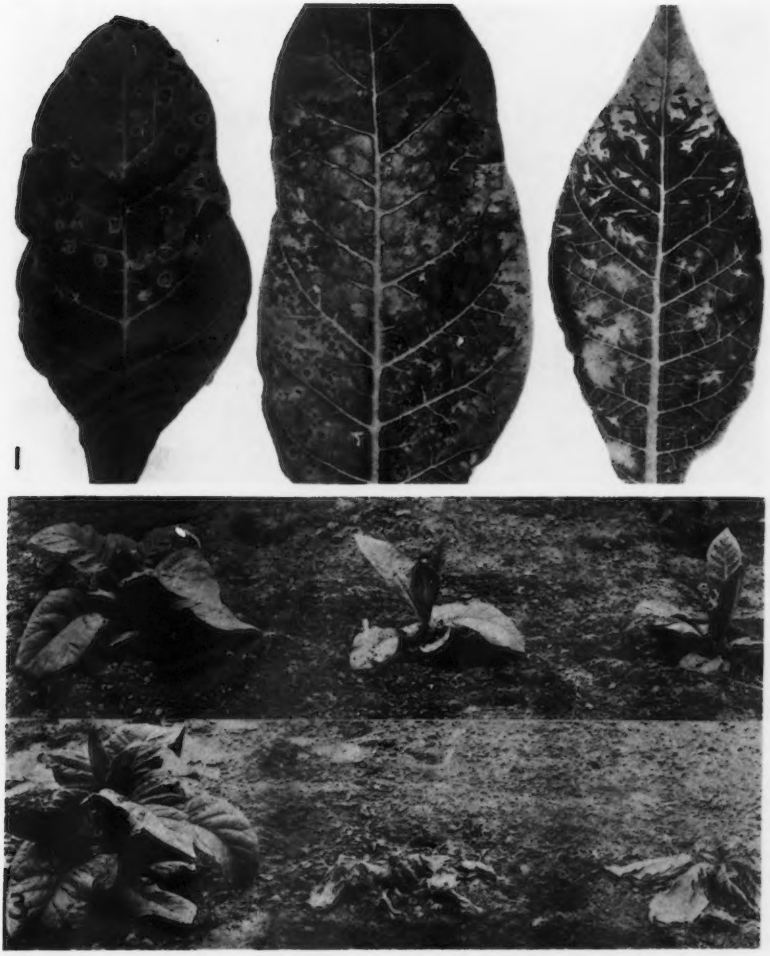


Tomato streak virus 1:—FIG. 1, *showing necrotic local lesions and systemic mottling as produced by Ontario strain on N. tabacum, var. White Burley.* FIG. 2, *showing necrotic local lesions and systemic necrosis as produced by tomato streak virus 1 on N. tabacum var. White Stem Orinoco.* FIG. 3, *yellow local lesions produced on zinnia by either tomato streak virus 1 or the Ontario strain. On a few occasions a slight necrosis developed in the yellow lesion.* FIG. 4, *showing necrotic local lesions and systemic necrosis (slight) on N. Langsdorfii.* FIG. 5, *white necrotic local lesion produced on buckwheat.* FIG. 6, *necrotic local lesions on N. glutinosa.* FIG. 7, *necrotic local lesions on N. tabacum, var. White Burley.*



Tomato streak virus 1:—FIG. 1, *showing necrotic local lesions and systemic necrosis produced by tomato streak virus 1 on N. sylvestris.* FIG. 2, *showing necrotic local lesions and systemic mottling with necrosis as produced on N. sylvestris by Ontario strain of tomato streak virus 1.* FIG. 3, *necrotic local lesions as produced on petunia by either the tomato streak virus 1 or the Ontario strain.* FIG. 4, *large local lesions on petunia sometimes produced when mature lower leaves are inoculated.* FIG 5, *upper, showing systemic necrosis on petunia as produced by either tomato streak virus 1 or the Ontario strain; lower, systemic mottling as produced by tobacco virus 1.*



Tomato streak virus 1:—All figures of tobacco, variety Adcock, growing in the field. FIG. 1, *left, shows necrotic local lesions on inoculated leaf, centre, systemic mottling with necrosis on same plant; right, systemic mottling only on tip leaves of same plant. All three symptoms the result of inoculation with Ontario strain of tomato virus 1.* FIG. 2, *tomato streak virus 1 (Ontario strain); left, healthy check, and two plants to right show necrotic local lesions with systemic mottling. Note dwarfing.* FIG. 3, *tomato streak virus 1; left, healthy check; centre and right, two inoculated plants. Note inoculated plants are dead. First symptoms on these plants comprised necrotic local lesions, followed later by systemic necrosis.*

VARIETAL TESTING FOR THE REACTION OF OATS TO DISEASES, ESPECIALLY COVERED SMUT[1]

By O. S. Aamodt[2] and A. W. Platt[3]

Abstract

Artificial inoculation of oat varieties was carried on for a period of five years. Sixty-one varieties of oats were tested in replicated plots for two years and thirteen for three years with a composite collection of inoculum of the covered smut organism, *Ustilago levis* (Kell. and Swingle) Mag. All gradations in reaction from high susceptibility to apparent immunity were found to exist.

Dehulling the kernels previous to inoculation increased the incidence of smut approximately six times. Susceptible varieties gave relatively greater increases in smut when dehulled than did resistant varieties. The increase in smut obtained by dehulling was independent of the year in which the test was conducted.

There were no significant differences in the total amount of smut obtained between any two of the seasons in which the tests were conducted but the season influenced the relative varietal reaction.

Natural epidemics of halo-blight *(Pseudomonas corona-faciens* (Ch. Elliott) Stev.) and blast (cause unknown) provided opportunities for obtaining data on the reaction of a large number of oat varieties. Immunity from neither of these diseases was observed but marked varietal differences were noted.

Introduction

As a prerequisite to a breeding program for disease resistance in oats, it was desirable to obtain information on the reaction of varieties to the diseases present in Alberta. According to the reports on the "Prevalence of Plant Diseases in Canada" (3, 4, 15) the most common and destructive diseases of oats in Alberta are probably covered smut, caused by *Ustilago levis* (Kell and Swingle) Mag., halo-blight, caused by *Pseudomonas coronafaciens* (Ch. Elliott) Stev., and blast, the specific cause of which is unknown. It is reported that from 20 to 46% of the fields examined for covered smut were found to contain smut and that percentages as high as 30 were recorded. Halo-blight is reported as common practically every year, with the severity of the attack and the consequent damage varying with the year from no apparent damage to light general damage. Not much information is available as to the loss in yield attributable to this disease.

Covered Smut *(Ustilago levis)*

Literature Review

No attempt has been made to review in any detail the literature on covered smut of oats. That portion of the literature dealing with aspects of the subject under discussion in this paper will be mentioned.

[1] *Manuscript received September 26, 1936.*

Contribution from the Department of Field Crops, University of Alberta, Edmonton, Canada, with financial assistance from the National Research Council of Canada. This paper was presented, in part, before the Canadian Phytopathological Society Meeting at Edmonton, June, 1935.

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Reed (16) in 1920 reviewed the work of earlier authors on the subject of the comparative resistance of oat varieties to covered smut. In his own work he tested the reaction of seven host species and found that *Avena brevis*, Roth. and *A. strigosa* Schib. had smut-free plants, while *A. byzantina* C. Koch. was highly resistant. All other species were generally susceptible, although two varieties of common black oats were apparently immune Gaines (10) tested the reaction of some 210 varieties to covered smut and found that 21 of these were smut-free.

Dehulling the seed before inoculation has been shown by several workers (2, 11, 14, 19) to increase the amount of smut obtained. Johnston (14) found that this increase was greatest in susceptible varieties and least in resistant varieties.

Methods

Preliminary tests on the reaction of oat varieties to covered smut were commenced at Edmonton in 1930. In that year hulled* kernels of several oat varieties were inoculated with a composite collection of chlamydospores of the covered smut fungus, and seeded in 10-foot rows, 100 seeds per row. In 1931 the varieties were tested, both with the hull of the kernel removed before inoculation and with the hull of the kernel intact. These treatments were not replicated. In 1932, and in subsequent years, the treatments were similar to those described for 1931, except that they were in duplicate. In all tests the varieties were planted in a systematic order. This is not considered by the writers to invalidate the analysis of the data by variance, for differences due to positional effect are not likely to influence smut infection.

The inoculum used was a composite collection of smutted panicles gathered from places throughout the province and from the varietal tests at this station. The smutted panicles were of the covered type. The chlamydospores when examined under the microscope appeared to be typical *U. levis*. The smutted panicles gathered were passed through a meat grinder and the coarser chaff removed by sifting through a screen. Liberal and approximately equal amounts of inoculum were added to each lot of seed.

Reed (17) has shown that physiologic forms of *U. levis* exist. A detailed study of distribution and prevalence of physiologic forms of *U. levis* has not been made in Alberta. It is believed that the composite inoculum used in this investigation was a representative sample of the forms prevalent in the province.

The senior author (1) has discussed the use of composite cultures in testing the reaction of wheat varieties to *Tilletia levis* and *T. tritici*. In that investigation the results indicated that the use of composite collections of chlamydospores of the bunt fungi in testing the reaction of wheat varieties gave results that were sufficiently reliable for all practical purposes. While

* *Throughout this paper the current practice is being followed of referring to normal grain with the hull intact as "hulled", and to grain from which the hull has been removed artificially as "dehulled".*

the use of composite inoculum may be expected to bring in a possible deviation in the smut percentage from that which might have been obtained had pure cultures been used, it is believed that their use is warranted in establishing the relative susceptibility or resistance of oat varieties to covered smut.

The effect of variations in spore load were not studied in this investigation. Gaines (9) cites the work of Heald who showed that up to a certain maximum load, infection in wheat increases with an increase in spore load. In this investigation the aim has been to have the spore load above the optimum, and in this way eliminate a portion of the variations due to this factor. However, further investigations on the effect of spore load on covered smut infection in oats would appear to be well worth while.

Seeding was done each spring when the soil temperatures reached 60–65° F., as these temperatures have been shown by Johnston (14) to be the most favorable for infection.

At harvest time the plants were pulled and classified as smutted or smut-free. The percentage of smutted plants was calculated for each row.

Results

As the varieties were not replicated in the preliminary experiments of 1930 and 1931, the data obtained on varietal reaction in these tests will not be presented in this paper. These data showed, however, that there were marked varietal differences in reaction to covered smut. The varieties of *A. nuda* that were tested showed high susceptibility, the percentage of plants smutted ranging from 64 to 100. Those of *A sativa orientalis* were generally susceptible but less so than those of *A. nuda*. The varieties of *A. byzantina*, on the other hand, appeared quite resistant while those of *A. sativa* ranged from high susceptibility to apparent immunity.

Some 61 varieties representing various species were selected for further study. All of these varieties were tested for smut reaction in both 1932 and 1933, while 13 that were more promising from an agronomic standpoint were tested again in 1934.

Data on the smut reaction of 11 varieties of *A. sativa* and 2 varieties of *A. sativa orientalis* for the three-year period, 1932–34, are presented in Table I, while data on the smut reaction of 41 varieties of *A. sativa* and 7 varieties of *A. byzantina* for the two-year period, 1932–33, are presented in Table II. In Table I the mean smut percentage for the two-year period 1932–33 is given in addition to the mean smut percentage for the three-year period, 1932–34. Thus the smut percentage of any of the 13 varieties listed in this table is directly comparable with those of any of the 48 varieties listed in Table II. In view of the different infection rates of hulled and dehulled seed, which are discussed later in the paper, the standard errors of the individual treatment averages, as well as the general mean for each variety, are given below Tables I and II. This will enable the reader to estimate readily the significance of the observed differences between varieties obtained with either hulled or dehulled seed.

TABLE I

COVERED SMUT, HALO-BLIGHT AND BLAST REACTIONS OF OAT VARIETIES

Variety	C.A.N.†	Percentage covered smut*											% halo-blight			% blast 1929
		Hulls not removed					Hulls removed									
		1932	1933	1934	Av. 1932–33	Av. 1932–34	1932	1933	1934	Av. 1932–33	Av. 1932–34	Mean 1932–33	Mean 1932–34	1930	1931	Av.	
Avena sativa																	
Victory	518	12.5	34.0	12.5	23.3	19.7	69.5	79.5	74.5	74.5	74.5	48.9	47.1	25	25	25.0	12.3
Banner	62	5.5	28.5	15.5	17.0	16.5	55.0	79.0	65.0	67.0	66.3	42.0	41.4	5	8	6.5	—
Legacy	460	4.0	15.5	10.5	9.8	10.0	73.5	66.5	68.0	70.0	69.3	39.9	39.7	—	—	—	—
Alaska	458	10.5	6.0	16.5	8.3	11.0	67.5	59.5	61.0	63.5	62.7	35.9	36.8	15	15	15.0	—
White Cross	601	1.5	7.5	15.5	4.5	8.2	61.5	28.5	71.0	45.0	53.7	24.8	30.9	20	12	16.0	24.0
Gopher	14	2.0	3.0	7.5	2.5	4.2	46.0	22.5	67.0	34.3	45.2	18.4	24.7	5	15	10.0	24.0
Accession No. 1	—	11.5	0.5	2.0	6.0	4.7	29.0	41.5	39.5	35.3	36.7	20.6	20.7	—	—	—	—
Accession No. 2	—	14.0	0.0	0.0	7.0	4.7	12.0	5.5	6.5	8.8	8.0	7.9	6.3	—	—	—	—
Accession No. 3	—	1.0	0.0	0.0	0.5	0.3	3.0	4.5	1.0	3.8	2.8	2.1	1.6	—	—	—	—
O.A.C. 144	39	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	10	10.0	—
Markton	67	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	12	11.0	11.9
A. sativa orientalis																	
New Era	181	13.0	13.0	29.5	13.0	18.5	90.5	85.5	93.5	88.0	89.8	50.5	54.2	—	—	—	—
Leader	199	23.0	25.5	23.5	24.3	24.0	74.0	72.5	80.5	73.3	75.7	48.8	49.8	15	18	16.5	—

	Hulls not removed	*Hulls removed*	*General mean*
S.E. of percent covered smut infection, 1932–34, is	*±2.31*	*±4.89*	*±2.71*
S.E. of the difference of two such means is	*±3.27*	*±6.81*	*±3.83*

† *Canadian Accession number.*

* *Each value is the average of duplicate determinations.*

TABLE II

COVERED SMUT, HALO-BLIGHT AND BLAST REACTIONS OF OAT VARIETIES

Variety	C.A.N.*	Percentage covered smut**							% halo-blight			% blast, 1929
		Hulls not removed			Hulls removed			Mean 1932–33				
		1932	1933	Av.	1932	1933	Av.		1930	1931	Av.	
A. sativa												
Accession No. 4	—	22.5	0.5	11.5	74.5	89.0	81.8	46.6	—	—	—	—
Rainbow	361	1.5	27.0	14.3	76.5	79.0	77.8	46.0	—	—	—	—
Colorado No. 37	301	0.0	21.5	10.8	74.5	72.5	73.5	42.1	25	12	18.5	25.6
Russian No. 76	448	9.0	13.0	11.0	81.0	65.0	73.0	42.0	—	—	—	—
Star	467	12.0	12.0	12.0	53.5	57.0	55.3	33.6	—	—	—	—
Cole	493	5.5	10.0	7.8	54.0	51.5	52.8	30.3	5	5	5.0	10.9
Iogold	139	0.0	9.5	4.8	60.0	25.0	42.5	23.6	8	3	5.5	10.3
Richland	4	0.0	9.5	4.8	5.0	65.0	35.0	19.9	20	20	20.0	21.0
Iowar	5	0.0	3.0	1.5	35.0	39.5	37.3	19.4	3	5	4.0	11.6
Madrid	325	2.0	1.5	1.8	36.5	34.0	35.3	18.5	3	8	5.5	31.3
Iowar	—	4.0	3.0	3.5	15.0	39.5	27.3	15.4	—	—	—	—
Kherson	255	0.0	2.0	1.0	20.5	28.0	24.3	12.6	—	—	—	—
Green Russian	246	3.0	1.5	2.3	25.0	16.5	20.8	11.5	5	10	7.5	18.0
North Finnish	510	3.0	0.0	1.5	20.0	17.0	18.5	10.0	5	10	7.5	5.5
Terry	282	1.5	0.0	0.8	17.0	21.0	19.0	9.9	5	8	6.5	9.2
Loviscaptonia	—	2.5	0.0	1.3	9.0	10.0	9.5	5.4	—	—	—	—
Accession No. 1	—	2.0	1.5	1.8	11.0	7.0	9.0	5.4	—	—	—	—
White Maine	289	0.5	1.5	1.0	7.5	4.0	5.8	3.4	10	10	10.0	21.0
Keystone	254	0.0	0.0	0.0	9.0	1.5	5.3	2.6	3	5	4.0	7.5
Svalof	—	1.0	0.0	0.5	5.5	0.0	2.8	1.6	5	8	6.5	—
Ferguson Navarro	234	0.0	0.0	0.0	6.0	0.0	3.0	1.5	0	5	2.5	34.5
Scottish Chief	275	0.0	0.0	0.0	2.0	2.5	2.3	1.1	25	12	18.5	17.7
Dwarf Culberson	231	0.5	0.0	0.3	4.0	0.0	2.0	1.1	0	3	1.5	4.8
Hatchett	247	1.0	0.5	0.8	2.0	0.0	1.0	0.9	3	3	3.0	3.7
Black Bell No. 1	176	0.0	0.0	0.0	1.5	2.0	1.8	0.9	0	8	4.0	16.3
Monarch	260	0.0	0.0	0.0	3.0	0.0	1.5	0.8	10	10	10.0	6.9
Yellow Russian	476	0.0	0.0	0.0	2.0	1.0	1.5	0.8	3	8	5.5	—
Pringles Progress	267	0.5	0.0	0.3	2.0	0.0	1.0	0.6	50	50	50.0	12.9
O.A.C. No. 72	468	0.0	0.0	0.0	1.5	0.0	0.8	0.4	3	3	3.0	—
Bicknell	223	0.0	0.0	0.0	1.0	0.0	0.5	0.3	3	3	3.0	6.5
Kanota	253	0.0	0.0	0.0	1.0	0.0	0.5	0.3	3	3	3.0	2.0
Aurora	64	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	3	1.5	24.9
Awnless Monarch	60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25	15	20.0	7.9
Black Diamond	115	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15	12	13.5	9.8
Black Mesdag	432	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	20	15.0	2.6
Cornellian	435	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	10	10.0	26.5
Cornellian	302	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	8	5.5	15.4
Early Ripe	496	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25	20	22.5	—
Frazier	233	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3	3	3.0	1.2
Nortex	263	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	3	1.5	5.8
Teck	280	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	3	1.5	—
A. byzantina												
Awnless rustproof	160	0.0	0.0	0.0	21.0	2.5	11.8	5.9	25	20	22.5	0.3
Fulghum	2	0.0	0.0	0.0	0.5	1.0	0.8	0.4	5	8	6.5	0.7
Black Algerian	174	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	1	0.5	4.4
Burt	299	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5	5	5.0	8.4
Cassel	452	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	8	4.0	—
Red Algerian	270	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10	8	9.0	2.1
Red rustproof	514	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0	1	0.5	5.6

	Hulls not removed	*Hulls removed*	*General mean*
**Canadian Accession Number.*			
***Each value is the average of duplicate counts.*			
S.E. of the mean percent covered smut is	*±1.80*	*±3.66*	*±2.03*
S.E. of the difference of two such means is	*±2.54*	*±5.18*	*±2.87*

The analysis of variance as developed by Fisher (8) has been used for the treatment of the data obtained in this investigation. An analysis of variance was calculated from the data obtained from the 61 varieties listed in Tables I and II for the two-year period 1932–33. The results are presented in Table III. In addition, an analysis of variance was calculated from the data obtained from the 13 varieties listed in Table I for the three-year period, 1932–34. The results are presented in Table IV. The significance of the mean square of any possible variant compared with the mean square for error, was determined by the method given by Snedecor (18). As the results obtained in each of the analyses are quite similar, they will be discussed together as far as possible.

The magnitude of the mean squares for varieties in relation to that of the mean squares for error (Tables III and IV) indicates that all varieties are not genetically alike in their reaction to covered smut. When comparing the mean smut percentage for the period 1932–34 of the varieties listed in Table I, it will be noted that Victory, Banner and Legacy were highly susceptible; White Cross and Gopher were significantly lower in mean smut percentage than the above three varieties, but were nevertheless quite susceptible. Alaska was significantly more susceptible than Gopher but less so than Victory. O.A.C. 144 and Markton appeared to be immune from the covered smut collections used in these investigations. The two varieties of *A. sativa orientalis*, New Era and Leader, were both highly susceptible. When considering the mean percentage smut for the two-year period 1932–33 of the varieties listed in Tables I and II, it will be noted that the varieties of *A. sativa* range from high susceptibility to apparent immunity. Of the 52 varieties representing this species, six had a mean smut percentage of over 40%, seven had 20 to 40%, seven had 10 to 20%, twelve had 1 to 10%, eight had less than 1% and twelve failed to show any smut. Five of the seven varieties of *A. byzantina* tested were apparently immune, while the remaining two were highly resistant.

The results obtained show that there is already in existence a wealth of varieties that possess a high degree of resistance to covered smut. Unfortunately none of these varieties are agronomically suitable for Alberta. The most commonly grown variety, Victory, was one of the most susceptible varieties tested, while Gopher, which is the least susceptible of the recommended varieties, was moderately susceptible, having 24.7% infection. With these results in mind it is not difficult to understand why it is that covered smut is so prevalent in commercial oat fields.

The smut obtained on plants grown from hulled seed was much less than that obtained on plants grown from dehulled seed. That this difference in smutted plants is statistically significant is shown by the highly significant mean squares obtained for treatments compared with those obtained for errors (Tables III and IV). The mean smut percentages obtained on 61 varieties for the two-year period 1932–33 were 3.5%, for hulled seed, and 21.3% for dehulled seed. The thirteen varieties grown for the three-year

TABLE III

ANALYSIS OF VARIANCE OF PERCENTAGE COVERED SMUT ON OAT VARIETIES, 1932–33

Variation due to	Degrees of freedom	Sums of squares	Mean square	F
Years	1	11	11	0.2
Treatments	1	38,669	38,669	1171.7*
Varieties	60	131,620	21,940	664.8*
Varieties × years	60	3,412	57	1.7*
Varieties × treatments	60	63,503	1,058	32.1*
Treatments × years	1	126	126	3.8
Varieties × treatments × years	60	9,126	152	4.6*
Error	244	8,111	33	–
Total	487	254,578		

* *Exceeds the 1% point.*

TABLE IV

ANALYSIS OF VARIANCE OF PERCENTAGE COVERED SMUT ON OAT VARIETIES, 1932–34

Variation due to	Degrees of freedom	Sums of squares	Mean square	F
Years	2	352	176	2.0
Treatments	1	49,541	49,541	563.0*
Varieties	12	56,633	4,719	53.6*
Varieties × years	24	4,578	191	2.2*
Varieties × treatments	12	23,260	1,938	22.0*
Treatments × years	2	252	126	1.4
Varieties × treatments × years	24	2,418	101	1.1
Error	78	6,838	88	–
Total	155	143,872		

* *Exceeds the 1% point.*

period 1932–34 showed percentages of 9.3 and 45.0 for hulled and dehulled seed respectively. These results are in agreement with those obtained by other workers (2, 11, 14, 19).

The increase in smut that may be expected, due to the removal of the hull, is dependent on the varieties used. This is shown by the significant mean squares obtained for the interaction of varieties and treatments compared with those obtained for errors (Tables III and IV). That is, the varietal differences were not the same under the two conditions of treatment, namely, hulled and dehulled seed. The differences given in Table V between the percentages of smut in the two treatments for each variety were obtained by subtracting the smut percentage, calculated by totalling the means of duplicate determinations for three years, of hulls not removed from that obtained in a similar manner with hulls removed. The standard error of the difference between two such differences would be $\sqrt{\frac{88 \times 3 \times 2 \times 2}{2}}$, or 22.98. Cross

differences in excess of 45.96 may be judged to be significant. Thus the cross differences between all the more susceptible varieties and Accessions No. 2 and No. 3 are significant.

These results clearly show that the susceptible varieties gave relatively greater increases in smut when dehulled than did the resistant varieties, indicating a more favorable response to dehulling. These results agree with those obtained by Johnston (14) who has shown also that certain oat varieties owe their apparent resistance to the mechanical protection afforded by their hulls, while other varieties have resistance that is independent of the presence or absence of the hull. Such results are substantiated in the present investigation. In all cases where smut occurred, the percentage smut obtained when the hull was removed was greater than that obtained when the hull was intact, except in the case of Accession No. 2 in 1932. Thus it would appear that in these varieties the hull acts as a protective organ. Other varieties, however, failed to show smut regardless of whether the hull had been removed or not. It would therefore appear that this latter group has resistance to, rather than protection from smut infection.

TABLE V

DIFFERENCES BETWEEN TOTAL SMUT PERCENTAGES WITH HULLS REMOVED AND HULLS NOT REMOVED*

Variety	Difference
Victory	164.5
Banner	149.5
Legacy	170.0
Alaska	155.0
White Cross	136.5
Gopher	123.0
Accession No. 1	96.0
Accession No. 2	10.0
Accession No. 3	7.5
O.A.C. 144	0
Markton	0
New Era	214.0
Leader	155.0

** Total differences for three years of the mean of duplicate determinations.*

Cross differences in excess of 45.96 may be judged to be significant.

Johnson (13) has shown that it is possible to transfer the resistance of agronomically inferior varieties to agronomically superior varieties without difficulty. The question arises as to whether the plant breeder should use hulled or dehulled seed, or both, in testing the reaction of varieties and hybrid selections to covered smut. The production of new smut-resistant varieties should have as its objective the production of varieties that have inherent physiological resistance rather than mere mechanical protection from infection, since a variety having only mechanical protection may become infected when grown commercially, owing to injuries sustained by the hull during threshing operations. The writers have not failed to recognize that there may be also a mechanical barrier to natural inoculation in the field when the caryopsis is developing within the hull and the smut spores are being blown about by the wind. The high percentage of smut commonly observed in commercial oat fields compared with that obtained in artificial tests using hulled seed, suggests that threshing injuries sustained by the hull must be one of the chief factors involved. Resistance in a variety or hybrid population

can be determined with surety only when the complicating factor of the mechanical protection of the hull is removed. Dehulling sufficient kernels to obtain reliable indices of infection is both tedious and costly, when a large number of varieties or hybrid selections are to be tested. Such a procedure is to be avoided if possible. An examination of the data in Tables I and II reveals that when tested for two years, 1932–33, only eleven of the 61 varieties failed to show smut when grown from hulled seed, but these smutted when grown from dehulled seed. Consequently, it would seem that when the object of the investigation is the discovery of resistance in a variety or hybrid selection, it would be a good procedure to test all the material, using hulled seed, eliminating any that are smutted and retesting the remainder, using dehulled seed.

There were no significant differences in the total amount of smut obtained between any two of the seasons in which the tests were conducted. This is shown by the non-significant mean squares for years compared with those for errors, (Tables III and IV). It would appear that the environmental factors that influence the incidence of this disease were sufficiently constant over the three-year period of this test not to influence the amount of smut obtained.

The mean squares obtained for the interaction of years and treatments compared with those obtained for errors were not significant (Tables III and IV). This indicates that the increase in smut obtained by removing the hull is independent of the year in which the test was made. If conditions were such that the amount of smut obtained varied markedly with the year, it is possible that this relation would not hold.

When considering the data obtained on the 13 varieties tested for the three-year period 1932–34 it was found that the relative varietal reaction was influenced by the season, as is shown by the significant mean square obtained for interaction (Table IV). The F value for the comparison of the mean square of varieties with that of varieties $\times$ years ($F = 24.7$) greatly exceeds the 1% point. This shows that varietal reaction generally was consistent from year to year for most of the varieties. The data in Table III, for the 61 varieties tested for the two year period 1932–33, show that the mean square of varieties $\times$ years compared with that of error was also significant.

The significant mean square for interaction that was obtained means that certain varieties reacted differently to the conditions obtaining in any given year than did other varieties. By calculating the difference in percentage smut for each variety from the percentage smut of the same variety in the other two years, with a uniform correction being made for the average difference between all varieties in that year and the average of these varieties in the other years, and testing the cross differences obtained, it can be shown which varieties are reacting in a differential manner in each of the years. Such cross differences were calculated for the 13 varieties grown for the three-year period 1932–34. The data obtained are presented in Table VI. The standard error of the difference between any two cross differences is 27.6,

hence cross differences in excess of 55.2 may be considered significant. Accession No. 2 had a plus difference of 46.1 in 1932, while Banner had a minus difference of 60.9. The cross difference of 107.0 is highly significant, and clearly indicates a differential response. Thus conditions in 1932 seemed to be very suitable for infection of Accession No. 2 and unsuitable for Victory. In 1933 conditions were such as to favor infection and smut development on Victory and Banner, and under the same conditions infection was not favored on White Cross and Gopher. On the other hand, in 1934, this latter situation was reversed, as infection of White Cross and Gopher was favored and infection of Victory and Banner was not.

TABLE VI

DEVIATION OF SMUT PERCENTAGE OF FOUR COUNTS OF THE VARIETIES IN A GIVEN YEAR FROM THE AVERAGE SMUT PERCENTAGE OF THE SAME VARIETY IN THE OTHER TWO YEARS, MINUS THE DIFFERENCE BETWEEN THE AVERAGE SMUT PERCENTAGE OF ALL VARIETIES FOR THAT YEAR AND THE AVERAGE SMUT PERCENTAGE OF ALL VARIETIES IN THE OTHER TWO YEARS

Variety	Year		
	1932	1933	1934
New Era	− 8.4	−22.9	+31.3
Leader	− 1.9	− 1.4	+ 3.3
Victory	−30.4	+64.6	−34.2
Banner	−60.9	+80.6	−19.7
Legacy	+ 9.6	+14.6	−15.2
Alaska	+19.1	−17.9	− 1.2
White Cross	+ 9.6	−70.9	+61.3
Gopher	+ 2.1	−64.9	+62.8
Accession No. 1	+ 3.6	+ 8.8	−12.4
Accession No. 2	+46.1	−14.9	−31.2
Accession No. 3	+ 8.6	+10.6	−19.2
O.A.C. 144	+ 6.1	+ 6.6	−12.7
Markton	+ 6.1	+ 6.6	−12.7

The standard error of the difference between one total and the average of the others is 19.52.

The standard error of the difference of two such differences is 27.6.

Cross differences in excess of 55.2 may be judged to be significant.

The second order interaction of varieties × treatments × years for the 61 varieties tested for the two-year period 1932–33 is significant (Table III). This indicates that the differential effect of dehulling on the resistant and susceptible varieties was not consistent for the two years of the test. In Table IV the data show that for the 13 varieties tested for the three-year period 1932–34, the second order interaction was not significant.

The nature of the conditions that bring about these differential responses can only be a subject for speculation at the present time. Possibly the relation between the environmental factors in the maturation of the seed, and the growth rate of the varieties as affected by the season following infection are related factors. Whatever the reason for these differential reactions the fact is apparent that a much better index of the reaction of a given variety may be obtained when that variety is tested over a period of years, rather than in a single season.

Halo-Blight (*Pseudomonas coronafaciens*)

Literature Review

Investigations concerning varietal reaction of oats to halo-blight have been reported by Elliott (5). She was able to demonstrate that varieties differed in their reaction to this disease, but that all the varieties tested were attacked

to some extent and that the differences between varieties tended to become less marked as the severity of the attack was increased or as the season advanced.

Results

In 1930, and again in 1931, a natural epidemic of halo-blight occurred in the oat classification nursery at this station. Notes were taken on the reaction of each of the 188 varieties growing in the nursery by estimating the percentage of leaf area affected. The data obtained on those varieties, upon which a smut reaction was obtained also, are presented in Tables I and II. As the varieties were not replicated it is difficult to judge the significance of the results obtained. However, a highly significant coefficient of correlation of $+.797$ was secured between the indices of blight obtained in 1930 and those obtained in 1931. This indicates that the varietal reaction was reasonably consistent over this two-year period and that at least the larger differences between varieties, in amount of blight, may be regarded as significant.

In 1930 several of the varieties failed to show any symptoms of the disease, but in 1931 lesions were present on all of the varieties. It is thus apparent that immunity from this disease was not present in any of the varieties that were subjected to the epidemic. These results are similar to those obtained by Elliott (5). Moreover, there did not appear to be any distinct difference between the reactions of the various species tested. Lee, C.A.N. 255, a variety of *A. sativa*, Chinese Hulless, C.A.N. 225, a variety of *A. nuda*, and Black Algerian, C.A.N. 174, Culred, C.A.N. 454, and Red Rustproof, C.A.N. 514, varieties of *A. byzantina* appeared to be the most resistant, being blighted less than 1% on the average. Gartons' Yellow, C.A.N. 240, a variety of *A. sativa orientalis*, appeared to be the most susceptible, being given a rating of 72.5% blighted. Pringle's Progress C.A.N. 267, Upright C.A.N. 517, and Columbian C.A.N. 465, varieties of *A. sativa*, were also quite susceptible, having an infection rating of 50, 50 and 65% respectively.

It is interesting from a taxonomic point of view to note the difference in the amount of blight obtained on the common varieties Victory and Banner. Victory had 25.0% blight, while Banner had only 6.5%. It is difficult to distinguish between these varieties morphologically, but when an epidemic of halo-blight is present Victory is readily distinguishable from Banner by the greater number of halo-blight lesions present on the leaves.

Blast

Literature Review

The literature on blast has recently been reviewed by Huskins (12) and in consequence will not be dealt with at any length in this paper.

Elliott (6), while noting that blast was often associated with halo-blight in the field, showed that blast was not due to the blight but was probably favored by the same environmental factors. As a result of further work (7) she was able to show that varieties differed in the amount of blasting and that, while the amount of blasting varied greatly in different years, the relative

varietal reaction was reasonably consistent. Huskins (12) has called attention to possible genetic resistance to blast in certain oat varieties and to the possibility that these differences are not due to a general physiological correlation with panicle size.

Results

In 1929 a large amount of blasting occurred on the oat varieties grown at this station. Part of the data obtained on varietal reactions* are presented in Tables I and II. While these data are not sufficiently complete to allow for statistical evaluation it would appear that distinct varietal differences exist. There is a difference of approximately 34% in blasted florets between the most resistant and the most susceptible varieties. The magnitude of these differences suggests that they are real rather than apparent.

Two varieties of *A. byzantina*, Fulghum and Awnless Rustproof, appear to be the most resistant, while Ferguson Navarre, a variety of *A. sativa*, appears to be one of the most susceptible. White Cross and Gopher, two commonly grown varieties of *A. sativa*, also appear to be quite susceptible.

The percentage of blast on 97 oat varieties was correlated with the mean percentage of halo-blight on the same varieties. A non-significant coefficient of correlation of $+.190$ was obtained. If the values for blast and halo-blight infection used in obtaining this correlation truly represent the reactions of the varieties concerned, it would appear from the correlation value obtained that different sets of genetic factors are concerned in resistance to these two diseases.

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STUDIES ON THE CONTROL OF ROOT-ROT DISEASES OF CEREALS

IV. INFLUENCE OF MECHANICAL SEED INJURY ON INFECTION BY *FUSARIUM CULMORUM* IN WHEAT[1]

By J. E. Machacek[2] and F. J. Greaney[3]

Abstract

The results of field experiments made in 1932, 1933, and 1934, to determine the effect of mechanical seed injury on the incidence of root rot caused by *Fusarium culmorum* and on yield in wheat are presented.

Successful positive attacks of Fusarium root rot were experimentally induced in field plots. The tests showed that reduced emergence, increased root rot, and reduced yield uniformly followed the planting of injured wheat seed; and that the amount of disease increased and the yield decreased with an increase in the degree of seed injury. In these experiments Mindum and Marquis wheat seemed equally affected by seed injury.

The investigation suggests that the large annual losses in yield caused by root-rot diseases of cereals in Western Canada may be substantially reduced by sowing clean, vigorous, sound seed.

Introduction

A short account (4) of greenhouse and field experiments which were designed to determine the effect of mechanical seed injury on the incidence of Fusarium root rot in cereals was published in 1933. The greenhouse tests showed that seedlings arising from mechanically injured seed of wheat, oats, and barley were more frequently and severely attacked by *Fusarium culmorum* (W.G.Sm.) Sacc. than were seedlings from uninjured seed. The field tests (one year's results) demonstrated that the use of mechanically injured seed promoted the development of seedling blight and root rot in wheat, and thereby resulted in a retardation of plant growth and a reduction in yield. Continuing the field work of 1932, experiments were made at Winnipeg, Man., in 1933 and 1934. A summary of the three years' results is presented in this paper. The relevant literature on the subject of seed injury in wheat and other cereals has been reviewed in earlier papers (4, 5).

Experimental Methods

During the investigation, the following kinds of seed of Mindum and Marquis wheat were used: (1) Normal, sound seed (uninjured), (2) Lightly scarified seed (slightly injured), (3) Heavily scarified seed (severely injured).

Each experiment consisted of rod-row plots of injured and uninjured seed of these two varieties of wheat. One-half of each plot was artificially infested with *F. culmorum*.

The principles of randomization and replication were used in the design of the experiments and rendered possible valid tests of significance and experi-

[1] *Manuscript received October 27, 1936.*
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mental error. The data were analyzed by the procedure described by Fisher (1) as the analysis of variance. Details concerning plot arrangement, soil-infestation methods, and methods of recording the amount of disease infection in cereal root-rot experiments have already been presented (2).

In 1932 the seed coats were injured by rubbing the kernels with sandpaper. In 1933 and 1934 a small scarifying machine was used to injure the seed. The hand-made machine consisted of a wooden frame on which was mounted a small wooden roller, fitted with a hand crank, and an adjustable canvas apron which was pressed closely against one side of the roller. The roller and the surface of the apron facing the roller were covered with sandpaper. The kernels of wheat were passed between the revolving roller and the stationary apron. It was possible to obtain any required degree of injury to the seed by tightening or slackening the apron, and by passing the seed through the machine a given number of times.

The fungus *Fusarium culmorum* (W.G.Sm.) Sacc., which was originally isolated in 1930 from a rotted crown of Marquis wheat, was used to infest field plots in this study. Previous tests both in greenhouse and field had shown that this fungus was distinctly pathogenic to wheat.

Experimental Results

The value of the analysis of variance as a means of sorting out the effects of seed treatments, soil treatments, and varieties, and of eliminating irrelevant data in the experiments is illustrated in Table I. This table gives the complete analyses of variance for disease rating and yield data of the 1934 experiment.

TABLE I

ANALYSES OF VARIANCE. INJURED SEED EXPERIMENT, 1934

Variance due to	Degrees of freedom	Sum of squares	Mean square	Z	5% point
Disease Rating					
Blocks (between)	5	1,684.98	336.99		
Varieties	1	432.70	432.70	1.0167	0.9441
Error (a)	5	283.23	56.64		
Soil treatments	1	5,747.70	5,757.70	2.2141	0.8012
Soil treatments × varieties	1	52.54	52.54		
Error (b)	10	686.09	68.60		
Seed treatments	2	1,822.38	911.19	2.1210	0.7037
Seed treatments × varieties	2	4.08	2.04		
Seed treatments × soil treatments	2	40.58	20.29		
Seed treatments × varieties × soil treatments	2	23.05	11.52		
Error (c)	40	523.48	13.09		
Total	71	11,300.81			

TABLE I—*Concluded*

ANALYSES OF VARIANCE. INJURED SEED EXPERIMENT, 1934—*Concluded*

Variance due to	Degrees of freedom	Sum of squares	Mean square	Z	5% point
Yield					
Blocks (between)	5	1,237.08	247.42		
Varieties	1	4,371.12	4,371.12	2.5566	0.9441
Error (a)	5	131.29	26.25		
Soil treatments	1	3,954.56	3,954.56	2.4357	0.8012
Soil treatments × varieties	1	201.34	201.34		
Error (b)	10	303.38	30.33		
Seed treatments	2	1,272.07	636.03	1.7310	0.7037
Seed treatments × varieties	2	329.51	164.75		
Seed treatments × soil treatments	2	37.99	18.99		
Seed treatments × varieties × soil treatments	2	81.21	40.60		
Error (c)	40	797.87	19.95		
Total	71	12,717.42			

The analyses in Table I clearly establish significant differences, both with respect to disease rating and yield, between soil treatments, varieties, and seed treatments. In every instance the Z values are much greater than the 5% probability values. The results indicate, therefore, that a high degree of significance can be attached to differences in the amount of disease and yield observed in this experiment. A similar detailed examination was made of the data for 1932 and 1933. Standard errors for disease rating and yield for each of the three years are presented in the summary tables (Tables II, III, and IV).

Soil Treatments

It is known that the presence of a large and active natural fungus flora in soil has an appreciable influence on the development of parasitic fungi which attack the basal parts of cereal plants (3, 6, and others). On this account it is extremely difficult to determine to what extent the actual injury to a crop is caused by a particular organism introduced into a soil. To provide an adequate test of the effects of seed injury on the development of root rot caused by *F. culmorum*, the soil in one-half of the plots was experimentally infested with this organism. The experiments were designed so that differences in the amount of disease and in yield, arising from this type of soil treatment, could be properly evaluated. The importance of plot arrangement in cereal root-rot experiments has already been demonstrated elsewhere (2).

The effect on root-rot infection and on yield, of planting injured and uninjured seed of wheat in soil that was experimentally infested with *F. culmorum*, as well as in soil which was not, is shown in Table II.

TABLE II

EFFECT OF INTRODUCING *Fusarium culmorum* INTO THE SOIL OF FIELD PLOTS ON THE INCIDENCE OF ROOT ROT AND ON YIELD IN WHEAT IN 1932, 1933 AND 1934

Year	Soil treatment	Degree of seed injury			Mean	Z	5% point	Standard error of means
		Uninjured (control)	Slightly injured	Severely injured				
Disease Rating								
1932	Infested	72.1	—	77.4	74.7	1.69	0.72	0.90
	Control	66.1	—	68.2	67.2			
1933	Infested	91.3	93.7	96.9	94.0	2.98	0.71	1.02
	Control	60.5	67.1	69.4	65.7			
1934	Infested	70.4	77.6	81.6	76.5	2.21	0.80	1.38
	Control	52.2	58.0	65.7	58.6			
Yield (Bushels per acre)								
1932	Infested	33.4	—	29.7	31.5	1.52	0.72	0.96
	Control	38.9	—	35.7	37.3			
1933	Infested	10.6	6.5	2.9	6.7	2.75	0.71	0.56
	Control	19.7	19.9	17.3	19.0			
1934	Infested	20.0	12.1	10.9	14.3	2.44	0.80	0.92
	Control	34.9	28.7	23.9	29.2			

Severe attacks of Fusarium root rot were successfully induced in field plots of wheat in 1932, 1933 and 1934. The effectiveness of the method of applying mycelium and spores of *F. culmorum* to the seed and soil to induce a positive attack of root rot was established with a very high degree of probability. Each year the amount of root-rot infection was appreciably and significantly increased by artificial infestation of the soil. In 1933 and 1934 the yield difference between experimentally infested plots and those not so infested amounted to more than 12 bushels per acre.

Injured and Uninjured Seed

The evidence relating to the effect of planting mechanically injured seed in soil experimentally infested with *F. culmorum* and in ordinary field soil on the development of root rot and on yield in wheat is presented in Table III. During the three years 1932–34, the amount of root-rot infection was appreciably increased and the yield considerably decreased by sowing injured seed of Mindum and Marquis wheat. In all experiments the detrimental effects of planting injured seed in soil infested with *F. culmorum* were established with a high degree of significance. The results of 1933 and

TABLE III

EFFECT OF PLANTING MECHANICALLY INJURED SEED IN SOIL ARTIFICIALLY INFESTED WITH *Fusarium culmorum* AND IN ORDINARY FIELD SOIL ON THE INCIDENCE OF ROOT ROT AND ON YIELD IN WHEAT

Degree of mechanical seed injury	1932		1933		1934	
	Infested soil	Control soil	Infested soil	Control soil	Infested soil	Control soil
Disease Rating						
Uninjured	72.1	66.1	91.3	60.5	70.4	52.2
Slight	—	—	93.7	67.1	77.6	58.0
Severe	77.4	68.4	96.9	69.4	81.6	65.7
Standard error*	1.01		1.68		1.04	
Yield (Bushels per acre)						
Uninjured	33.4	38.9	10.6	19.7	20.0	34.9
Slight	—	—	6.5	19.9	12.1	28.7
Severe	29.7	35.7	2.9	17.3	10.9	23.9
Standard error*	1.51		1.22		1.29	

* *To be significant the difference between two quantities should exceed* $2 \times \sqrt{2} \times$ *standard error.*

1934 show that the amount of disease increased and the yield decreased with a progressive increase in the degree of injury. In 1932, experimentally infested plots planted with injured seed yielded 3.7 bushels per acre less than did plots sown with uninjured seed. The employment of severely injured seed in 1933 resulted in a loss of 7.7 bushels per acre; while in 1934 the yield loss per acre reached 9.1 bushels.

Varieties

Data showing the response of injured and uninjured seed of Mindum and Marquis wheat to root rot caused by *F. culmorum* are presented in Table IV. It is evident from this table that, in 1932 and 1933, Mindum was more susceptible to root rot than was Marquis. The significance of the difference observed in the amount of disease on these two varieties in 1934 is not clearly established. The results for 1932 and 1933 portray the most commonly occurring condition in Manitoba, for Mindum is usually more susceptible to Fusarium root rot than is Marquis. In both varieties and in all experiments the amount of disease was increased and the yield decreased by increasing the degree of injury. There is no conclusive evidence, however, that, as a result of mechanical injury to the seed, one variety suffered more than the other from root rot.

TABLE IV

THE EFFECT OF SEED INJURY ON MINDUM AND MARQUIS WHEAT IN RELATION TO THE INCIDENCE OF FUSARIUM ROOT ROT AND YIELD

Year	Variety	Degree of seed injury			Mean	Z	5% point	Standard error of means
		Uninjured (control)	Slightly injured	Severely injured				
Disease Rating								
1932	Mindum	72.4	—	76.4	74.4	1.68	0.86	1.26
	Marquis	65.8	—	69.3	67.6			
1933	Mindum	78 3	80.8	85.4	81.5	0.89	0.73	0.97
	Marquis	73.5	80.0	80.9	78.1			
1934	Mindum	58.6	65.7	71.1	65.1	1.02	0.94	1.25
	Marquis	64.0	67.8	73.6	68.5			
Yield (Bushels per acre)								
1932	Mindum	43.4	—	40.5	41.9	2.05	0.86	1.91
	Marquis	28.9	—	25.0	27.0			
1933	Mindum	13.6	11.5	7.8	11.0	1.29	0.73	0.70
	Marquis	16.7	14.9	12.2	14.6			
1934	Mindum	38.2	27.1	23.3	29.5	2.55	0.94	0.84
	Marquis	16.7	13.6	11.6	14.0			

Discussion

In relation to the subsequent crop, the main effect of seed injury, such as that caused by frost, drought, rust, and drastic chemical treatment is that the seedlings are less vigorous than are those from sound seed. The same is true of seed mechanically injured by threshing or scarification, but with the former types of injury the seed coat usually remains intact, and constitutes a barrier to fungus invasion; whereas in the case of mechanical injury the seed coat is ruptured, the endosperm is exposed, an easy avenue for fungus invasion is provided. This invasion may occur if the seed is stored under unfavorable conditions. In Western Canada, however, where storage conditions do not favor moldiness of grain, the invasion of the endosperm of injured seed by saprophytic and parasitic fungi is most likely to take place after the seed has been planted in the soil.

There is in the prairie soils of Western Canada a large and active fungus flora. Parasitic forms, particularly root-rotting fungi, are commonly present in all the major wheat-producing soils. These fungi can be expected to cause serious damage whenever environmental conditions favor their attack. As mechanical injury to the seed of wheat, and to the seed of other cereal crops, renders the endospermic nutrients accessible to saprophytic and parasitic

soil fungi, growth of these organisms is thus favored at the expense of the seedling plant with the result that plant emergence is reduced and a high percentage of the weak seedlings that do emerge fall an easy prey to the parasitic organisms. The final result is an appreciable reduction in yield.

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HEAT INDUCED TETRAPLOIDY IN BARLEY[1]

By F. H. Peto[2]

Abstract

A tetraploid sector on a barley spike was induced by germinating and growing barley for seven days at 35° C. Tetraploid and diploid florets from the same spike were compared with respect to chromosome pairing and chiasma formation.

Brief reference has already been made to a barley plant with a tetraploid sector produced in the summer of 1934 (1). In view of the interest shown by cytologists, it seems desirable to publish further details.

O.A.C. 21 barley was germinated and grown at 35° C. for seven days and subsequently carried to maturity under normal growth conditions. The treatment reduced germination to 62%, and 46% of the seedlings died, while the seedling growth rate of the remainder was severely checked.

The meiotic behavior of twenty of the above plants was studied and all but one found normal. In this plant both tetraploid and diploid florets were observed and their positions indicated that one side of the spike was tetraploid and the other side normal diploid. Chromosome doubling must therefore have occurred in a somatic division immediately subsequent to the differentiation of the primordium of the spike.

The occurrence of both tetraploid and diploid florets in the same spike afforded a unique opportunity for comparing these with respect to chromosome pairing and chiasma formation, since both types of florets had been exposed to identical internal as well as external environmental conditions and possessed identical genetical constitutions. Twelve nuclei of each of the two types of florets were analyzed and the data are given in Table I. The number of quadrivalents per nucleus varied from 1 to 7 with a mean of 3.58 while the number of bivalents varied from 2 to 12 with a mean of 6.75 On the average, approximately one-half of the chromosomes paired as quadrivalents and the other half as bivalents, with occasional univalents. Sixty-six cells were examined between mid-anaphase and early telophase in the heterotypic division; eleven of these had one pair of lagging chromosomes and two had three pairs of lagging chromosomes. Presumably most of these lagging chromosomes were the result of failure to pair, and a somewhat greater number of univalents might have been observed at metaphase had it been possible to analyze a larger number of nuclei.

The pairing in the diploid florets was very regular; seven bivalents were always present and all other meiotic stages were normal.

The number of chiasmata in the tetraploid nuclei should be double that observed in the diploid nuclei. Actually, 1.87 times as many chiasmata were present. Thus it appears that the presence of four instead of two

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TABLE I

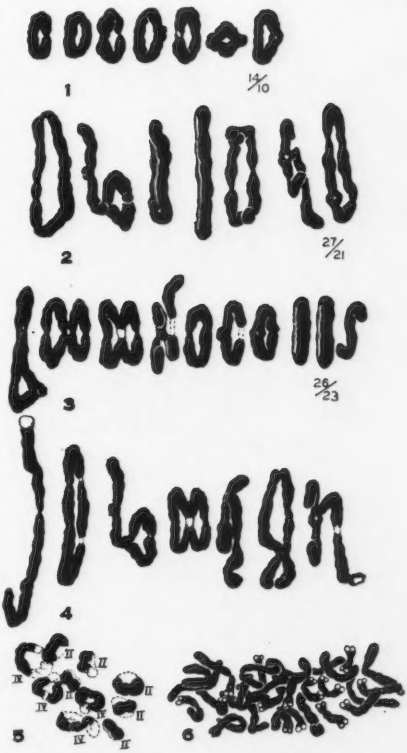
ANALYSIS OF HETEROTYPIC METAPHASE CONFIGURATIONS

No.	Univalents	Bivalents	Quadrivalents	Chasmata	
				Total	Terminal
			Tetraploid nuclei		
1	0	10	2	23	19
2	0	12	1	26	22
3	2	7	3	26	24
4	0	6	4	23	21
5	0	6	4	27	24
6	0	8	3	27	26
7	0	0	7	27	21
8	0	6	4	27	23
9	0	2	6	26	19
10	0	10	2	27	21
11	0	6	4	26	23
12	0	8	3	28	23
Total	2	81	43	313	266
Mean	0.17	6.75	3.58	26.08	22.17
			Diploid nuclei		
1		7		14	12
2		7		14	13
3		7		14	9
4		7		14	10
5		7		13	9
6		7		14	12
7		7		14	11
8		7		14	12
9		7		14	12
10		7		14	12
11		7		14	10
12		7		14	13
Total		84		167	135
Mean		7		13.92	10.41

homologous chromosomes caused only a very limited amount of interference in zygotene pairing. The random attraction of homologous regions at zygotene would account for the proportions of quadrivalents and bivalents observed. However, it is important to note that trivalents and single univalents never appeared. This would be expected on the assumption that prophase chromosomes are only attracted in pairs in any given homologous region. Consequently the pairing attraction throughout the whole chromosome length cannot be satisfied in trivalent formation. In any three chromosomes that tended to pair together at zygotene, there would always be at least half the length of one or two of them in which the attraction would be unsatisfied and these portions consequently would be free to pair with the fourth homologue.

Examples of diploid and tetraploid p.m.c. nuclei are shown in Figs. 1 to 3. Seven different types of quadrivalent associations are shown in Fig. 4 and represent almost all of the known types. Two tetraploid megaspore-mother cells were also analyzed; one contained seven quadrivalents and the other contained four quadrivalents and six bivalents (Fig. 5). The somatic tissues of the florets were also examined and chromosome counts taken wherever possible. A tetraploid nucleus from the nucellus is shown in Fig. 6.

It was unfortunate that this spike was completely used for cytological examination, otherwise there seems little doubt that a tetraploid strain of barley could have been established. However, the fact that a heat treatment during germination can induce somatic chromosome doubling in the primordium of a spike is of considerable importance. At the present time there is need for a satisfactory technique for conferring fertility on sterile F_1 hybrids by doubling the chromosome number in the primordia of spikes. This study gives some hope that such a technique can be developed.



FIGS. 1–6. FIG. 1. *Diploid pollen-mother cell, 7 bivalents.* FIG. 2. *Tetraploid p.m.c., 7 quadrivalents.* FIG. 3. *Tetraploid p.m.c., 4 quadrivalents and 6 bivalents.* FIG. 4. *Various types of quadrivalents.* FIG. 5. *Megaspore-mother cell, 4 quadrivalents and 6 bivalents.* FIG. 6. *Tetraploid nucleus from the nucellus. Magnifications* × *2000.*

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THE BIOLOGY OF *IPS PERTURBATUS* EICHHOFF[1]

BY A. R. GOBEIL[2]

Abstract

The biology of *Ips perturbatus* in the Gaspé Peninsula is described from observations made during the summer of 1933 and 1934. This species generally breeds on trees killed by *Dendroctonus piceaperda* Hopk. but was also found on white spruce dying from the attacks of *Diprion polytomum* Hartig. In the Gaspé peninsula there is one complete generation a year. At the end of September and the beginning of October, the young adults leave their host tree to hibernate in the ground. Emergence from the ground occurs in the spring.

Experiments show that the adult stage lasts nearly two years. During their first complete summer as adults, the females lay two sets of eggs. The following spring they lay a third set and die during the summer. There are one to four egg tunnels per engraving. The average number of eggs per egg tunnel decreases with the increase in the number of females per engraving. Dissection of 500 beetles indicates that the two sexes are present in about equal proportions. Analysis of the results of a population study made on a white spruce representing 48 feet of tree superficies attacked by *Ips perturbatus* produced the following results: 2448 egg tunnels, 22,512 young beetles, 58,800 egg niches and a mortality rate of 58.33%.

Coeloides dendroctoni Cushm. is the most important parasite of this species, but does not kill more than 5% of the larvae and pupae. No trace of woodpecker control was noticed.

Introduction

Of all the injurious forest insects, the Scolytidae are among those which have been most thoroughly studied by entomologists. In spite of that, however, we know very little of the biology of these insects. Indeed, in America, apart from some species belonging to the genus *Dendroctonus*, which have been quite well worked out, the majority of the representatives of the other genera were considered more or less of secondary economic importance, and their study has been neglected. We cannot foretell, however, whether certain species actually considered as secondary might not eventually, owing to certain conditions of environment or for other reasons, become of great economic importance.

Ips perturbatus is one of the Scolytidae generally referred to as secondary bark beetles and, except for a few short papers published during the last ten years by Swaine (24) and Watson (26 and 27), all the information about it found in the literature is purely of a taxonomic character.

The distribution of this insect is very wide; it has been found almost everywhere in Canada and "apparently follows the northern range of its host tree" (23).

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This paper was presented at McGill University, Montreal, in partial fulfilment of the requirements for the degree of Master of Science.

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The observations recorded in this paper were made during 1933 and 1934 in the Gaspé Peninsula, province of Quebec. The work was carried on in the vicinity of the Federal Mine which is situated 1750 feet above sea level near the middle of the Peninsula, *i.e.*, 50 miles northwest of the village of Grand Cascapedia. The district is very hilly, and some of the highest mountains of the province occur within five to ten miles from the Mine. These are: Mount Lyall, 3000 feet; Mount Sterling, 3100 feet; Hogsback, 2725 feet; Mount Richardson, 3885 feet; and Mount Albert, 3775 feet. In this type of country the summer is rather short and precipitation is high. Hence the seasonal history of the insect in this region may be expected to differ from that on the coast or in other parts of Canada.

I. Host Tree

A number of attempts were made to breed *Ips perturbatus* on healthy white spruce, balsam and black spruce, but none were successful. In nature, this insect has never been found by the writer on dying black spruce, but under cage conditions the females cut egg tunnels, laid eggs, and the larvae lived all summer. It is doubtful, however, whether they could reach the adult stage before the advent of the first snowfall.

In 1933 and 1934, *Ips perturbatus* was found on white spruce that had been killed or much weakened generally by *Dendroctonus piceaperda* Hopk., or less often by *Diprion polytomum* Hartig. It enters the upper part of the trunk the year following the *Dendroctonus* attack. Thus, during the summer of 1934, *Ips* was found on trees that had been infested by *Dendroctonus* in June and July, 1933.

Although at the decline of a *Dendroctonus* outbreak, *Ips* is often as numerous as the *Dendroctonus*, it is not always found in the upper part of every tree killed by the latter. Indeed, if the latter species is present on more than half the total length of the trunk, the bark then seems to be too dry, and the portion of the trunk free from *Dendroctonus* is generally infested by *Dryocoetes affaber* Mannh. (see Table I, Trees 9, 12). In other cases, although the upper part of the tree presents suitable conditions for *Ips* infestation, examination reveals the presence of *Polygraphus rufipennis* Ky. only (Table I, Trees 7, 8, 10, 11). This is due to the fact that often *Polygraphus* enters the tree during the same year as *Dendroctonus*. Simpson (20) reports that, at Fredericton, N.B., *P. rufipennis* breeds three times during the same summer, in June, July and at the end of August. In the Gaspé, the number of broods of this species was not determined, but many adults were seen flying at the end of August. At that time of the year, it enters the trees infested by *Dendroctonus* in June of the same season, so that when *Ips* emerges the following spring, its place in many trees suitable for attack is already taken by *Polygraphus rufipennis*.

Twelve trees killed by *Dendroctonus* were cut, and the trunks were examined to gain a general idea of the distribution of secondary bark beetles on the

different portions of the trunk and the type of trees preferred by each species, especially by *Ips perturbatus*. Table I shows the distribution of the different species of bark beetles in these trees.

The zones do not end abruptly; between zones there is an intermediate portion, one to three feet in length, in which the species of the two adjacent zones are intermixed.

Where *Ips perturbatus* and *Ips borealis* are found together on a portion of the trunk, as in Trees 1, 2, and 4, *I. perturbatus* is always the predominant species.

TABLE I

DISTRIBUTION OF SECONDARY BARK BEETLES ON THE TRUNK OF WHITE SPRUCE KILLED BY *Dendroctonus piceaperda*

Tree No.	D.B.H., in.	Total length, feet	*Dendr.* zone, feet	Other secondary bark beetles
1	13	61	28	*Ips pert.*, *Ips borealis* and *Dr. affaber* 14 ft., dia. 9–6 in.; *Ips borealis* only 24 ft., dia. 6–1 in.
2	8	48	16	*Ips pert.* and *I. borealis* 18 ft., dia. 6–4 in.; *Ips borealis* 12 ft., dia. 4–1 in.
3	12	72	22	*I. pert.* 14 ft., dia. 8-6 in.; *I. borealis* 10 ft., dia. 3–1 in.; *P. rufipennis* 26 ft.
4	11	69	26	*I. pert.* and *I. bor.* 28 ft., dia. 8–3 in.; *I. borealis* 13 ft., dia. 3–1 in.
5	12	67	27	*I. pert.* 22 ft., dia. 8–4 in.; *I. borealis* 16 ft., dia. 4–1 in.
6	9	66	13	*I. pert.* 32 ft., dia. 7–4 in.; *I. borealis* 18 ft. last 3 ft., *Pityophthorus* sp.
7	11	65	30	*Polygraphus rufipennis* 33 ft.
8	10	55	20	*Polygraphus rufipennis* 32 ft.
9	10	51	31	*Dryocoetes affaber* 18 ft. (tree very dry).
10	11	75	34	*Polygraphus rufipennis* 39 ft.
11	12	74	25	*Polygraphus rufipennis* 47 ft.
12	11	68	40	*Dryocoetes affaber* 25 ft.

Table I shows that *Ips perturbatus* generally attacks the portion of the trunk situated between the diameters of eight and four inches. In the upper part, its distribution is limited by the thinness of the bark. We might be inclined to believe that just the opposite condition limits their distribution on the lower part, but this is not the case; and if *Ips* is rarely found at the base of the trunk, it is because it generally goes to trees killed by *Dendroctonus*, *i.e.*, trees whose bases are already infested when *Ips* enters them. But in some other cases, for example in trees almost completely defoliated by *Diprion polytomum*, *Ips* is found at the base of the trunk. Thus on July 17, many *Ips perturbatus* tunnels were found at breast height on a tree of about 10 inches D. B. H. which, although much weakened by the saw-fly attacks, still bore green needles even on the lower branches. A more careful examination of the same tree, made on August 29, revealed the presence of *Ips perturbatus* for at least the first 40 feet of the trunk. Other secondary scolytids, such as *Ips borealis* Sw., *Dryocoetes affaber* Mannh. and *Trypodendron bivit-*

tatum Ky. were conjointly inhabiting the same portion of the trunk, but in much smaller numbers. On August 30, many other saw-fly-infested trees were examined and three of them were found severely infested by *Ips perturbatus* for the first 20 basal feet of the trunk. These trees were dead then, but they had certainly been alive in the spring, since it was still possible to see at the top of the tree the spring foliage which was, at the end of August, of a yellowish color.

We may conclude that in general *Ips perturbatus* follows *Dendroctonus* distribution, being noticeable one or two years after the appearance of *Dendroctonus*. When the *Dendroctonus* outbreak is at its peak, *Ips* has not attained its maximum numbers but does so when *Dendroctonus* is on its descending trend. By that time it is probably as numerous or even more numerous than *Dendroctonus*, but the decrease of the latter means also a decrease in the number of trees, on which *Ips* is able to live, so that its diminution will be as rapid as that of *Dendroctonus*. In Gaspé, however, a very interesting and particular case seems to occur. In 1934, while *Dendroctonus* was on its decline and *Ips* was probably at its maximum density, the number of trees infested by *Dendroctonus* not being sufficient for the *Ips*, many of the latter attacked white spruce severely defoliated by the saw-fly. As the trunks of these trees were absolutely free from *Dendroctonus*, *Ips* entered them at the very base and its population per tree was doubled. Therefore, it appears that in the absence of trees killed by *Dendroctonus*, those defoliated by the spruce saw-fly are in a condition suitable to *Ips perturbatus*. This case, however, is peculiar to the Gaspé Peninsula where two outbreaks, namely, of *Dendroctonus piceaperda* and of *Diprion polytomum*, exist concurrently. For this reason, it should be very interesting to follow the progress of *Ips perturbatus* in that particular district.

II. Bionomics

A. Adult

1. Teneral Period

A tree, infested by *Ips perturbatus* in early June, was cut at the beginning of July and examined about twice a week by removing small pieces of bark. The first newly transformed adults were found on July 30, but they were few in number. On August 1 and 2, however, about 25% of the pupae had reached the adult stage. The young beetles fed very extensively; they obtained their food solely from the fibre of the bark, changing it to a kind of brown dust and leaving the larval mines and pupal cells almost unrecognizable.

On August 4, a log three feet long obtained from the tree under observation, was placed two feet above the ground, and a mat surrounded by "tanglefoot" was placed underneath to catch the beetles as they emerged. It was thought then that they would feed for a month or so and, consequently, would leave their host by the beginning of September. However, they did not leave the log until September 22. This seems to show that, around Kelly's camp, the young adults feed for about seven weeks before they emerge from their host. Of course, this statement applies only to the young beetles

that reach the adult stage early in August. If the pupae transform to adults only at the beginning of September, as some do, they cannot feed much more than a month before the advent of the first snow, at which time they leave their host; these younger beetles can be recognized in the following spring by their paler brown color.

Occasionally some pupae do not reach the adult stage until the middle or end of September. In this case, the young beetles are still very immature at the time of the first snows and, as they are generally unable to hibernate in the tree, they die during the winter. Some observers have expressed the belief that the young adults could emerge from their host towards the end of July, and that there were two generations a year or at least one and a partial second, but the above study indicates that such is not the case in the Gaspé Peninsula.

2. Emergence from Host-tree and Hibernation

Many Scolytidae, such as *Dendroctonus* and *Dryocoetes*, pass the winter as larvae or adults in their host tree under the bark. Others, such as *Ips perturbatus* and *I. borealis*, leave their host in the fall and hibernate on the ground in the moss. This habit, however, is not common to all the species of the genus *Ips;* thus *Ips longidens*, like *Dendroctonus*, hibernates in the larval or adult stage under the bark where it matured (3).

It was believed for a long time that *Ips perturbatus*, like many Scolytidae, passes the winter in the host tree. To the best of my knowledge, Watson (26) was the first and the only worker to give correct information on the hibernating place of this species. Working in Algoma district, Ontario, he found that they overwinter as adults, after leaving their tunnels in September and October to hide in the ground.

With few exceptions, the same habit obtains in the Gaspé. The larvae in general reach the adult stage between the first week of August and the beginning of September. As said before, the young beetles feed for $1\frac{1}{2}$–2 months and then drill through the bark to make an orifice, or "exit hole" of the same diameter as that of the entrance hole bored a few months previously by the parent beetles. In winter, a tree which has been severely infested by *Ips perturbatus* during the summer, is completely free of living insects of this species. The young beetles, which have matured too late in the fall to leave their host before the fall of the first snow, are always killed by the low winter temperature and are found dead under the bark the following spring.

Early in the spring, large numbers of beetles can be found in the moss beneath the tree they had attacked during the previous year. Many beetles are also found in the detritus scattered on the ground, under the bark of fallen trees, in the crevices of old stumps or other obstacles which stop the insects in their fall before they reach the ground. Some are present even in old *Dendroctonus* tunnels at the base of the infested tree.

In general, it can be said that the beetles leave their host tree in the fall to hibernate in the ground. However, if a tree infested by *Ips perturbatus* is cut during the summer, although the majority of the adults will leave the tree in the fall, quite a number will hibernate in their host and emerge from it the following spring. This was observed last spring when several living adults were found under the bark of a tree attacked by *Ips perturbatus* in the previous year and cut during the same summer. The same phenomenon was also observed in another tree presenting exactly the same conditions. Concluding then that even in standing trees a few adults might succeed in wintering, I immediately cut two trees infested by *Ips* during the previous year. Not a single living beetle was found in either of them. It may be assumed, that in standing trees these insects cannot, at least in that particular district, resist the low temperatures of the open during the winter. It is probable for this reason that, when an infested tree lies on the ground, the adults which have not left the tree before the advent of the first snow succeed in hibernating in their host tree.

In order to secure exact information as to the time of exodus of the young beetles from their host, a large mat was nailed on a wooden frame (Fig. 1), constructed during the middle of the summer, at the base of a tree attacked

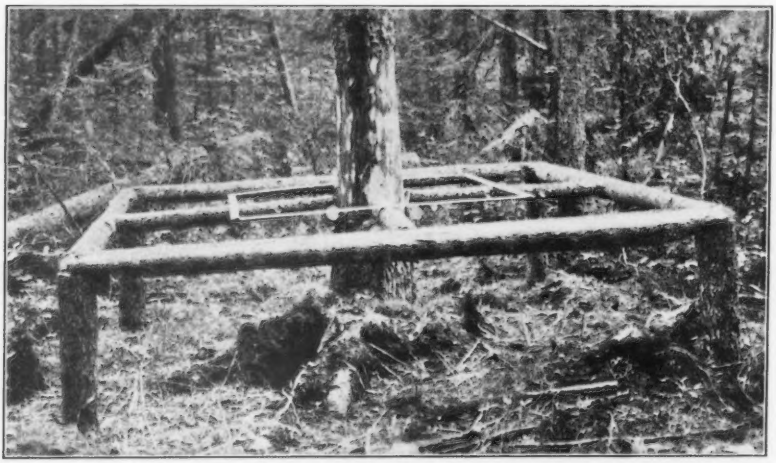


FIG. 1. *Wooden frame (on which a mat was nailed) used for records of Ips perturbatus emergence in the fall.*

by *Dendroctonus* and subsequently infested by *Ips perturbatus*. The frame formed a square 8 × 8 ft., and the small joists on which the mat of factory cotton was nailed were two feet above the ground. A band of tanglefoot two inches wide surrounded the mat, while another band was also placed on the mat around the base of the tree to prevent the beetles from climbing the trunk. A third band of tanglefoot surrounding the tree itself was placed

one foot above the mat. This third band was used to determine whether the adults, when they leave their exit holes, simply fall from the tree or crawl down the trunk as some of Watson's observations in Ontario seemed to indicate.

This mat was constructed by August 23, and was examined at least twice a day, generally at 11.45 a.m. and 5 p.m. Table II shows the daily emergence from August 24 to September 28.

TABLE II

EMERGENCE PERIOD OF *Ips perturbatus* IN THE FALL

Date	Old parent beetles	Young adults	Date	Old parent beetles	Young adults	Date	Old parent beetles	Young adults
Aug. 24	26	—	Sept. 5	6	—	Sept. 17	1	—
Aug. 25	10	—	Sept 6	1	—	Sept. 18	—	—
Aug. 26	4	—	Sept. 7	2	—	Sept. 19	10	—
Aug. 27	5	—	Sept. 8	1	—	Sept. 20	3	1
Aug. 28	2	—	Sept. 9	—	—	Sept. 21	3	2
Aug. 29	1	—	Sept. 10	1	—	Sept. 22	—	—
Aug. 30	2	—	Sept. 11	—	—	Sept. 23	4	6
Aug. 31	7	—	Sept. 12	1	—	Sept. 24	1	6
Sept. 1	—	—	Sept. 13	1	—	Sept. 25	—	7
Sept. 2	1	—	Sept. 14	—	—	Sept. 26	2	15
Sept. 3	—	—	Sept. 15	—	—	Sept. 27	4	14
Sept. 4	14	—	Sept. 16	2	—			

The young adults began to abandon their host in appreciable numbers on September 23. However, the great majority probably emerged at the beginning of October. As I was forced to leave the district on September 28, the daily examinations had to be discontinued.

Although no young beetles left their host before September 20, the emergence records for each day are given from August 23 to show that there is, during the entire summer, a more or less continuous emergence of the old, black, parent beetles. At the end of August, however, these beetles did not go to new trees to lay more eggs as they do in July; they merely hid themselves from the light in the folds of the mat. The old beetles leave their tunnels before the young adults, simply because they have been feeding during the entire summer.

No beetles were found in the band of tanglefoot placed on the mat around the tree or in the one surrounding the trunk of the tree itself. It can therefore be assumed that the insect does not crawl down the trunk but simply lets itself drop to the ground. On leaning trees, however, it might be possible, as suggested by Watson, that the beetles crawl down the trunk from the exit hole.

The number of beetles which left the tree after September 20 is certainly greater than that indicated by the records. The action of the wind and the rebounding of the insect from one branch to another may cause it to fall much farther from the trunk than four feet. Nevertheless, the table gives a good idea of the beginning of the emergence and its rate of increase.

It was also discovered that these insects, although very small, could pass through a band of tanglefoot two inches wide after a few hours of struggle; this was the reason for inspecting the mat twice a day and sometimes oftener at the end of September. The majority of the beetles were found in the folds formed at the corner of the mat. It is apparent, therefore, that in the construction of apparatus of this kind for the study of bark-beetles, a board two to three inches wide should be nailed around the mat. The beetles would be more easily caught in such a device since they would hide themselves under the board. A narrow band of tanglefoot on the board would increase the efficiency of the trap.

3. Spring Emergence

Ips perturbatus emerges in the spring as soon as the snow has disappeared and the ground is thawed.

Two emergence cages were constructed to follow the period of emergence. One of the two, Cage A, was built on the slope while the other, Cage B, was set in the valley. These cages (Fig. 2) measured 2 × 2 × 2 ft., and each was

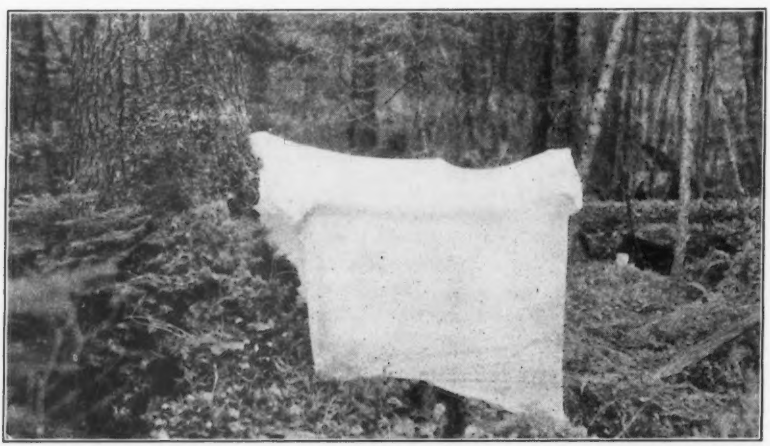


FIG. 2. *Spring emergence cage for Ips perturbatus.*

placed at the base of a tree. The cheesecloth covering was kept in place by tacks lightly driven into each corner post to facilitate its daily removal for the liberation of the beetles. As soon as the beetles come out of the ground, they are attracted by the light, go to the top of the cage, and gather in the folds of the cheesecloth, especially at the upper corners. They were collected late every afternoon.

The results obtained from these cages seem to show that, other factors being equal, the beginning of the emergence period varies with the topography of the site, being earlier on the east slope than in the valley. Thus in Cage A, the first beetles emerged from the ground on June 3, while in the

valley they were not observed until June 8, *i.e.*, five days later. It is quite possible that the daily period of insolation, being longer on the east slopes than in the valley, produces this accelerated or delayed emergence.

Table III shows the length of the emergence period in the valley and the number of *Ips perturbatus* collected every day in Cage B. The temperature and precipitation records for every day are also included, in order to show the relation between these two factors and emergence.

It can be seen from Table III that the emergence is intimately connected with the factor of precipitation. The temperature also influences the emergence period, but to estimate this influence properly, temperature records should also be taken under the moss within the cage. The second week of July was very warm, but at that time all the beetles had emerged from the ground, since none were found in the cage after July 11.

One may wonder whether the larvae that hatch from eggs laid by females emerging as late as July 11 will reach the adult stage early enough to leave their hosts before the advent of the first snow. This is dealt with in detail further on, but it can be said here that the progeny of parent beetles caged on July 9 reached the adult stage by September 7.

TABLE III

EMERGENCE PERIOD OF *Ips perturbatus* IN THE SPRING

Date	Emergence	Precipitation	Mean temperature at 4 ft. from the ground*	Date	Emergence	Precipitation	Mean temperature at 4 ft. from the ground*
June 8	44	—	43.25	June 25	—	0.04	55.30
June 9	—	Trace	43.25	June 26	—	—	53.25
June 10	64	—	53.00	June 27	2	—	51.00
June 11	—	0.30	50.85	June 28	7	—	54.10
June 12	—	Rain	51.85	June 29	—	0.55	55.80
June 13	—	Rain	46.40	June 30	—	—	52.75
June 14	—	Rain	45.15	July 1	16	—	52.30
June 15	—	0.68	45.55	July 2	—	0.74	57.00
June 16	—	—	48.25	July 3	—	0.04	55.80
June 17	46	—	52.00	July 4	8	0.38	57.45
June 18	—	0.09	54.40	July 5	11	0.06	55.25
June 19	31	—	58.20	July 6	4	—	61.75
June 20	—	0.70	49.85	July 7	—	0.48	61.50
June 21	43	—	54.70	July 8	1	—	55.70
June 22	—	0.30	53.30	July 9	9	—	57.55
June 23	—	—	52.45	July 10	4	—	56.65
June 24	20	1.98	57.25	July 11	3	—	62.30

* *The mean temperature was obtained by taking the average between the maximum and minimum temperature for each day.*

4. Entrance Hole and Entrance Tunnel

Ips perturbatus tunnels are not as a rule mixed with those of *Dendroctonus* except on a small section of the trunk in the intermediate zone. Its entrance holes are easily differentiated from those of *Dendroctonus* by the well known

resin tubes found around the entrance holes of *Dendroctonus* but never present around those of *Ips perturbatus*, since the latter attack the trees only when they are partly dry. Furthermore, the entrance holes of *Dendroctonus* are much larger than those of *Ips*, the former being 3.0 to 3.5 mm. in diameter while the latter measure only 2.0 mm. in diameter.

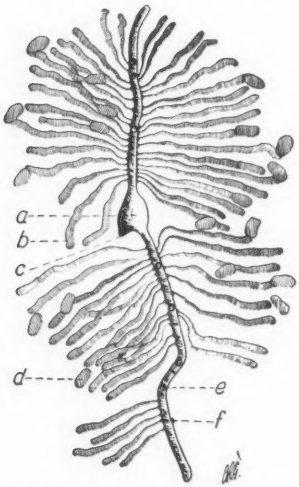


FIG. 3. *Ips perturbatus Eichhoff. General appearance of engraving with two egg tunnels.* ½ *natural size. (Original). a—nuptial chamber. b—larval mine. c—entrance tunnel. d—pupal cell. e—ventilation tunnel. f—egg niche.*

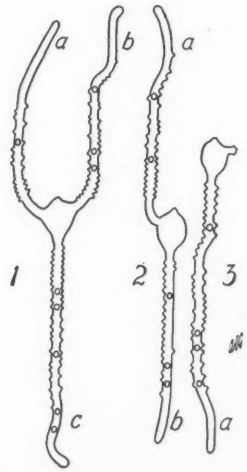


FIG. 4. *Ips perturbatus tunnels. (Original).* ½ *natural size. 1—Engraving with three egg tunnels, a, b, and c, (Triramous). 2—Engraving with two egg tunnels, a and b. Note that there are only three egg niches on the right side of tunnel b. Explanation on page 191 (Biramous). 3—Engraving with one egg tunnel, a (Uniramous).*

Quite often *Ips perturbatus* and *Ips borealis* share the same portion of the trunk. Their entrance holes are difficult to differentiate since they are almost of the same size. The entrance hole of *Ips borealis* has an average diameter of about 1.3 mm. while, as already said, that of *Ips perturbatus* measures 2.0 mm.

The entrance tunnel passes through the bark and leads to the nuptial chamber; its length varies with the thickness of the bark. On a standing tree these tunnels are always directed upward at an angle of 45 degrees. The diameter of the entrance tunnel, and of the egg gallery, is just large enough to admit the cylindrical body of the beetle. The entrance tunnels of *Ips perturbatus* are always cut by the males. Soon after the first beetles emerged last spring, a number of tunnels were opened, and wherever only one beetle was present it was removed and preserved in alcohol for sex determination at some later date. In 17 tunnels thus opened and found to contain only one adult in the nuptial chamber, all specimens proved to be males.

5. Nuptial Chamber

As stated in a previous chapter, the male cuts the entrance tunnel, excavates the nuptial chamber, and is then joined by from one to four females, each of which mines its own egg tunnel. The nuptial chamber is the central part of this subcortical dwelling place; all the passages formed by the egg galleries radiate from it. It is more or less triangular or sub-oval in shape and of quite constant size. The base of the isosceles triangle measures about 8 mm. and its height varies from 12 to 14 mm. The triangular shape is most striking in a triramous engraving, each egg gallery beginning at an angle of the geometrical figure (Fig. 4; 1). In a uniramous or biramous engraving, the nuptial chamber is more sub-oval in shape (Fig. 4; 2, 3). As Swaine (23) writes, the chamber is used for several purposes: "It serves as a temporary storage room for boring dust thrust into it by the females working in the egg-tunnels; it is also used by the beetles for turning or reversing their position, particularly by species which cut no ventilation-tunnels; and it is used regularly for copulation. With polygamous species the male spends nearly all his time in the nuptial chamber and in the entrance-tunnel".

6. Excavation of the Egg Tunnel and Food Tunnel

Several beetles were caged on June 10, and three days later when the cage was opened, the examination of the tunnels already started showed that one female had mined her egg tunnel to a length of 15 mm. and had excavated five egg niches on one side of it. This shows that as soon as the female has entered the nuptial chamber and copulated, she begins to cut the egg gallery and deposit eggs. This egg gallery is made partly in the wood and partly in the bark. In a biramous or triramous engraving, the egg tunnel opposite the entrance tunnel is generally cut by the first female to enter the nuptial chamber. Evidence of that is seen in uniramous engravings where the single egg tunnel is always situated opposite the entrance tunnel. This is also confirmed by the fact that in polygamous engravings the egg gallery opposite the entrance tunnel frequently contains more eggs than the others, probably because these eggs are laid by a young female which is laying her first set and, consequently, has entered the tree just after emergence early in the summer.

When a female has laid her first batch of eggs, she needs a period of feeding before starting to cut a second egg tunnel. For that, she simply continues to mine and prolong the egg tunnel, which then takes the name of food tunnel or "food burrow".

Some experiments were undertaken to show the rate at which the females bore their egg tunnels, and at the same time to obtain information on the length of the egg stage. Many beetles were put in cages of the type illustrated; the tunnels cut by these beetles were examined every three days and the distance excavated was measured. Sixteen cages were constructed, each of them containing from 8 to 10 adults. In some engravings the beetles, being disturbed, left their tunnels; others were killed when the cages were opened. In many tunnels, however, I was able to keep track of the work done

by the females for a period of more than a month. As expected there is a great variation in the distance excavated by the same female from one day to another, or by one female as compared with another. Some females mined only 13 to 14 mm. in three days, while others mined over 22 mm. in the the same period of time. Certain tunnels were left undisturbed for a month and when they were opened after that period, measured from 100 to 120 mm., while others had a total length of only 40 to 50 mm. These great variations, observed from one tunnel to another, are chiefly due to the different conditions found by the insect under the bark. But the daily variations in the length excavated by one female are mainly explained by differences in temperature, the insect being less active on cold days.

The information obtained on the egg stage is dealt with in another section of this paper.

7. Egg Niches

The female of *Ips perturbatus* deposits her eggs singly in small "niches" which she makes on each side of the egg tunnel. These niches, seen from above, have a triangular appearance, but from the side they appear cup-shaped. The lumen of the niche is of about 1.25 mm. long, while the depth varies from 1.0 to 1.25 mm. If we compare these proportions with the size of the egg, which is 1.06 mm. in length by 0.68 mm. in thickness, we find that the niche is much larger than the egg. This is necessary, however, since the egg is not simply deposited loosely in the niche, but is surrounded and packed in with dust by the female. This dust does not project into the egg tunnel, but simply fills the niche in such a way that the sides of the egg tunnels remain smooth.

Very often, especially at the beginning of the egg tunnel, there is only a short distance between adjacent niches. The niches are almost contiguous, and, as a matter of fact, I have counted as many as 20 egg niches in $1\frac{1}{2}$ inch. Since the opening averages 1.25 mm., there is a space of 0.5 mm. or less between two consecutive niches.

A peculiar and very interesting case is found when two egg tunnels of different engravings are adjacent, being separated by less than $\frac{1}{4}$ inch. In this case, the female which is the last to start the egg tunnel (Fig. 4; 2b) does not cut any egg niches on the side adjacent to the other tunnel, *i.e.*, the right side in Fig. 4; 2b, probably because she is aware of the other female burrowing in the adjacent tunnel. Tunnels of that kind with all or most of the egg niches constructed on one side and none or merely a few here and there on the other side were often found.

Occasionally, although the egg tunnel may be quite long, the egg niches are not numerous and are widely separated one from the other. This may be due to the fact that the female which excavated this egg gallery was an old adult, which had already laid one or two sets of eggs before, and consequently had its power of reproduction much reduced. However, this subject requires further study.

8. Ventilation Tunnels

These are burrows placed at irregular intervals in the roof of the egg gallery and perpendicular to it. They may extend to or nearly to the outer surface of the bark or only halfway through it. There is no rule for their distribution and number; sometimes in a long egg gallery of three to four inches only one or two are present, while in other short galleries four or five may be found very near one another (Fig. 4; 1, 2, 3).

There are different opinions on the purpose of these tunnels which are present in the egg galleries of many species of Scolytidae. Some authors believe that they serve only for the aeration of the egg tunnel. Barbey (1) agrees with Chewyreuv that they serve the purpose of the nuptial chamber and he calls them "encoches d'accouplement" or copulation niches. He writes that: "Chewyreuv, ayant observé des Scolytides et Hylesines mis en élevage sous vitres, a pu constater que ces cavités n'avaient d'autre but que de permettre au mâle de s'accoupler pendant le forage de la gallerie de ponte." Swaine (23) states that they are used as "turning niches" for the female while she lays her eggs and as storage places for boring dust. Hopkins (12) believes that they serve for ventilation of the gallery and as storage places. There is probably some truth in all these statements. They may serve for ventilation but not exclusively for that purpose, since some of them do not go through the bark. Furthermore, unlike the *Dendroctonus* galleries, which often contain a mixture of resin and dust packed in the egg tunnel, the *Ips* galleries are, as a rule, always kept clean and have good aeration from the entrance tunnel. It is also probable that the so-called ventilation tunnels may serve for copulation as claimed by Chewyreuv and Barbey or as turning niches while the female lays her eggs. But, if this be their only purpose, it is difficult to understand why some should be found in the food tunnels where no eggs are laid. Even in these food tunnels they do not always serve for ventilation or as an opening to eject dust since some of them end bluntly in the bark. There is probably something more to be known about these tunnels.

9. Fertility and Longevity

It seems to be quite a common habit for many scolytid females to excavate more than one egg tunnel in the same season. Swaine (24) states that apparently *Ips perturbatus* and *Ips borealis* Sw. cut two egg tunnels in the same summer. Watson (27) wrote that *Dendroctonus piceaperda* (Hopk. lays two sets of eggs in the same season. Simpson (20) records *Polygraphus rufipennis* Ky. as cutting three egg tunnels in the same year and a fourth one in the following spring before death. He also found (21) that the female *Dendroctonus simplex* Lec. lays three sets of eggs during the same season. De Leon and Bedard and Terrell (8) working on *Dendroctonus monticolae* Hopk. found that two egg tunnels are cut by the females during the same summer.

To gather further information on that point in so far as *Ips perturbatus* Eichh. is concerned, a log of 12 inches in diameter and 3 feet long, heavily infested by *Ips perturbatus* on June 4 and 5, was caged on July 5 with another

log 7 inches in diameter and 39 inches long, obtained from a tree blown down by the wind the previous winter and free of any kind of bark-beetle attack. At that time (the beginning of July), the beetles were well established in the infested log and some eggs had already hatched. These two logs when peeled on September 5, revealed 42 egg tunnels in the fresh stick while the original infested log contained 106 egg tunnels. The result indicates then that 40% of the females left the original stick and entered the fresh one to lay a second set of eggs. In reality the percentage should have been much higher, since the infested log was not caged until a month after the original infestation and it is very probable that some females had already left the log when the latter was placed in the cage. Moreover, some females, after they had completed their first egg tunnel, might have come out and started to cut a second egg gallery on the same log instead of entering the fresh stick. Nevertheless, the experiment shows that a high proportion of the females, if not all of them, lay two sets of eggs in the same season.

Many old parent beetles—differentiated from the young by the black color—leave their host tree in the fall to pass a second winter in the ground. Thirty-six of these old black beetles were kept separately in the moss to determine whether they would die during the winter or emerge again in the following spring and lay more eggs. Of these beetles, 13 were living the following spring (1934). On June 4, they were placed in three holes, $\frac{1}{2}$ inch square, made in the bark of a log of spruce obtained from the top of a tree attacked by *Dendroctonus* the previous year. Each hole was covered with celluloid fastened to the bark with adhesive tape. When the log was examined on August 9, two egg galleries were found, one containing eight egg niches and the other ten; the progeny at that time were pupae and full-grown larvae. All the old parent beetles were dead in the galleries. The reason why only two egg tunnels were excavated may be partly that only a small proportion of the surviving beetles were of the female sex.

The conclusions of these experiments are:

1. That the females of *Ips perturbatus* lay two sets of eggs during the same season.

2. That the reproductive power of the female is greatly reduced following the second period of hibernation.

3. That the adult stage in some instances lasts nearly two years, the old parent beetles hibernating in the ground the second year to lay a third set of eggs and dying during the summer.

10. Relation between Fecundity and Proportion of Sexes in the Engravings

If the bark of a tree infested by *Ips perturbatus* is removed, we find numerous nuptial chambers, each of them used as rallying place for two, three or even four females, each mining her own egg tunnel.

Between the middle of July and the beginning of August, two trees were peeled and studied to provide an exact idea of the proportion of the females in the different types of brood burrows and the average number of eggs laid

per gallery for each type. Often the egg tunnels of two different engravings unite and are mixed over a part of their length. This occurs chiefly when the density of attack is great. All such engravings occurring on definite regions of the trunk were studied except those not distinctly separated from one another.

Table IV presents in summary the data derived from a careful study of 87 engravings. It can be seen from the figures presented in this table that *(a)* the biramous engravings are the most commonly found, *(b)* the average

TABLE IV

RESULTS OF THE STUDY OF 87 ENGRAVINGS OF *Ips perturbatus*

Type of engraving	%	Average no. of eggs per engraving	Average no. of eggs per egg tunnel	Average length of the egg tunnel
(a) *Tree No. 1:—Tree examined between July 13 and 15. 37 engravings or 70 egg tunnels yielding a total of 2138 eggs*				
Uniramous engraving	40.5	37.7	37.7	2.92
Biramous engrav.	32.4	60.8	30.4	2.66
Triramous engrav.	24.3	86.4	28.8	2.66
Quadriramous engrav.	2.7	101.0	25.25	2.25
Average		58.68	32.80	2.75
(b) *Tree No. 2:—Tree examined between Aug. 6 and 10. 50 engravings or 95 egg tunnels yielding a total of 2614 eggs*				
Uniramous engraving	34.0	35.00	35.00	3.25
Biramous engrav.	46.0	62.40	31.20	3.01
Triramous engrav.	16.0	75.00	25.00	2.83
Quadriramous engrav.	4.0	75.48	18.87	2.20
Average		55.62	31.00	3.00
(c) *Total average:—87 engravings or 165 egg tunnels yielding a total of 4752 eggs*				
Uniramous engraving	36.8	36.2	36.2	
Biramous engrav.	40.2	61.8	30.9	
Triramous engrav.	19.6	79.8	26.6	
Quadriramous engrav.	3.4	86.4	21.6	
Average		57.0	31.8	

number of eggs per egg tunnel decreases with the number of females per engraving, *(c)* the number of eggs per egg tunnel averages, on the whole, approximately 32.

Tree No. 2 was studied two weeks later than Tree No. 1. During this period the females were feeding all the time, thus increasing the length of the egg tunnels. This explains why the average length of the egg tunnels is higher in the latter tree and also why the total average length was not included in part "c" of the table.

As just stated the highest average number of eggs per egg tunnel is found in the uniramous engraving; the average decreases as the number of females per engraving increases. The decrease in the fecundity is not, however, directly due to the proportion of the sexes in the brood burrows, since small numbers of eggs were sometimes found even in uniramous engravings. The reason is to be found in the fact that in brood burrows of two, three or four egg galleries, the probabilities are two to four times greater that one of the females will be excavating her second or even third egg tunnel, *i.e.*, that she will have her reproductive power greatly reduced (see page 194). We also know that the male, after he has constructed the nuptial chamber early in the spring, is soon joined by the females. In a uniramous engraving there is a greater chance that this first and single female, which joins the male at the beginning of the season, will be laying her first batch of eggs and will consequently be able to produce the maximum number of eggs. Table V

TABLE V

NUMBER OF EGG NICHES PER EGG TUNNEL IN THE DIFFERENT TYPES OF ENGRAVINGS

Number of eggs per egg tunnel	Occurrence in the different types of engravings							
	Uniramous		Biramous		Triramous		Quadriramous	
	No.	%	No.	%	No.	%	No.	%
1 - 10	0	0	2	2.8	3	6.0	1	8.4
11 - 20	1	3.1	10	14.1	10	20.0	6	50.0
21 - 30	6	18.8	23	32.4	22	44.0	3	25.0
31 - 40	17	53.1	19	26.8	9	18.0	2	16.6
41 - 50	5	15.7	8	11.2	6	12.0	0	0
51 - 60	2	6.2	5	7.1	0	0	0	0
61 - 70	1	3.1	4	5.6	0	0	0	0

shows that large numbers of eggs per egg tunnel were not limited to the uniramous engravings, although on the whole the females under monogamic conditions produce more eggs than under conditions of bigamy or polygamy.

Sixty-nine is the greatest number of eggs observed in one egg tunnel. These were found in a biramous engraving. The smallest number was six eggs, found in a branch of a triramous engraving. Table V shows that the majority of the uniramous engravings contain between 31 and 40 eggs; the biramous 21–40, while the average for the triramous lies between 21 and 30, and for the quadriramous engravings between 11 and 20.

11. Numerical Relation of Sexes

From what has been observed in the brood burrows, there occur nearly two females for each male. However, the dissection of 500 young beetles, obtained from the same portion of a tree, revealed about an equal number of males and females, namely 242 females and 258 males, or 48% and 51.6%.

Blackman (2) working on *Pityogenes hopkinsi* Sw., explains this anomaly between the actual counts and what is found in the brood burrows by two factors:— *(a)* some males die bachelors in their nuptial chamber, not suc-

ceeding in attracting any females, *(b)* the male is preyed upon by predaceous birds and insects while he is making the entrance tunnel, or he may be washed from his burrow by beating rain. There is probably some truth in Blackman's statements, but these factors alone can certainly not explain the disproportion of nearly two females to each male found in the brood burrows of *Ips perturbatus*. It is also doubtful that they can explain the disproportion, which is sometimes even greater, in the brood burrows of all the polygamous species of bark-beetles. Although I have stripped the bark of many trees infested with *Ips perturbatus*, and examined hundreds of engravings, I cannot recall ever having found even a single burrow containing an unaccompanied male. However, in order to explain, even if only in part, the disproportion of 2 or 3 females to 1 male found in brood burrows of polygamous species the proportion of bachelor burrows should be quite high. With regard to the second factor, in so far as *Ips perturbatus* is concerned, the influence of predaceous birds and insects amounts to almost nothing; *Ips perturbatus* is usually found where *Dendroctonus* occurs, and the woodpeckers, which are the most effective predaceous birds, are much more busy working on the comparatively big and plump *Dendroctonus* larvae than on small *Ips* mining their entrance tunnel in the upper part of the tree.

It appears to me that this disporportion of the two sexes in the brood burrows of polygamous species of Scolytidae could be understood readily if we consider two facts common to many polygamous species: *(a)* that among polygamous scolytids, the entrance tunnel is excavated by the male, *(b)* that the female lays more than one set of eggs during the same season. Nusslin (16), Blackman (2), Escherich (11) and others have noted that among the polygamous species, the entrance tunnel is cut by the male. On the other hand, as stated previously (9), many workers have also observed that among certain species of Scolytidae the female cuts more than one egg tunnel during the same season. The observations made by the writer on *Ips perturbatus* in the Gaspé Peninsula show that these two statements hold for the species. From all these observations we may legitimately conclude the following: The male digs the entrance tunnel and is soon joined by the female who cuts the egg tunnel and lays one complement of eggs. When the first egg tunnel is completed, this female feeds for a time and then leaves that particular brood burrow to start a second egg tunnel elsewhere. She cannot, however, like *Dendroctonus piceaperda* or other monogamous species, cut her own entrance tunnel and she has to look for one already made by a male. It generally happens, then, that she finds the latter already established with one or two females, but apparently the male readily receives this new arrival.

Therefore, although the total number of males and females is about equal, *Ips perturbatus* practices polygamy because each female cuts two egg tunnels during the same season and must rely on the male for the excavation of an entrance tunnel. As the latter digs only one of these entrance tunnels at the beginning of the summer, we arrive at an approximation of two egg tunnels per engraving.

B. The Egg

The length of the egg stage, like the length of all the following stages, varies with the temperature under which development occurs. The first beetles began to emerge, in 1934, on June 3 and 4. Some were noted on a log on June 4, but most of the tunnels opened at that time contained only one adult, always a male. On June 5, many females entered the tunnels where they started to lay their eggs on June 6 and 7. The tunnels on that particular log were examined every two days but, the first larvae were not found until June 24. Hence, the eggs laid at the beginning of June took from 17 to 18 days to hatch.

The period of oviposition lasts about a month and a half, from the beginning of June to the middle of July. The period of incubation for eggs laid in July was not observed but, the daily temperature in July being higher than in June, the period of incubation should not be more than two weeks.

C. The Larva

1. Larval Mines

The larvae excavate their mines in the inner layers of the bark only. They do not score the wood as do the females when they cut their egg tunnels. Each larva burrows its own mine and the mines are always distinctly separated one from the other. They are filled with a dark brown frass which the larvae leave behind as they progress in their work. When the bark is removed from the tree, this frass makes the larval mines very conspicuous and easy to follow. They are more or less perpendicular to the egg gallery for the greater part of their length but towards the end they are often directed either upwards or downwards.

At their base, the larval mines are almost linear, but they increase in width as the larva grows and when the latter is full-grown the mine is nearly 2.0 mm. wide (Fig. 3; b). There is a great variation in the length of the mines; some measure only 40 mm., while others are as long as 80 or 90 mm. They are generally longer when the density of the population is low; thus if only a few beetles are caged on a log, the tunnels may reach 90 mm., but if the tree is heavily infested, the larval mines are rarely longer than 60 mm.

2. Length of the Larval Stage

The appearance of the first larvae was observed on June 24, and since some pupae were found on July 21, we may conclude that the larval stage lasts about four weeks. As the temperature at the end of June is about the same as that of the end of August in the Gaspé Peninsula, the length of the larval stage does not vary much, whether the eggs be laid early or late in the summer.

D. The Pupa

When full-grown, the larva makes the pupal chamber or pupal cell and then ceases to feed. This pupal cell, which is generally located at the end of the larval mine, is an oval cell with rounded ends (Fig. 3, d). It is constructed entirely in the bark and is about 3 mm. wide $\times$ 6 mm. long and 1.5 mm. deep.

The first pupae were noticed last summer on July 21. At that time many full-grown larvae, ready to pupate and easily recognized by their milky white color, were taken from a log and placed in a tin box between two moist pieces of bark. Four of these larvae pupated on July 25. They were then removed and transferred on another piece of bark to a pupal cell previously made by other larvae. That bark was also kept on wet moss in a tin box and the piece of wood, which was originally covered by the bark, was fitted exactly and placed on top; thus the pupae were kept as nearly as possible under natural conditions. One of these pupae reached the adult stage on August 2, and the others on the following day.

The same observations were repeated at the end of August on full-grown larvae, which had developed from eggs laid at the beginning of July. Six of these larvae pupated on August 23 and reached the adult stage as follows: one on September 5, four on September 7, and one on September 8.

These two observations made at different times during the summer show that at Kelly's camp in 1934 the pupal stage, at the end of July, lasted only eight to nine days, while by the end of August and the beginning of September, when the daily average temperature was much lower, the pupal stage was as long as 14 to 16 days.

E. Complete Duration of the Post-embryonic Development

Many beetles were caged at different periods of the summer and left undisturbed for 1½ to 2 months. When the tunnels made by these beetles were examined at the end of this period, most of the young were only full-grown larvae or pupae. They were then allowed to complete their development to the adult stage. In this manner, exact data were obtained as to the length of time required for the complete developmental cycle.

On June 3, many beetles were observed entering a log lying on the side of the road. This log was well exposed to the action of the sun. On July 29, the first beetles to be seen that summer were found on that log, but they were not very numerous before the beginning of August.

The beetles obtained from the emergence cages on July 9 were caged on a tree blown down by the wind the previous winter. When their tunnels were opened a month and half later (Aug. 20), many full-grown larvae were found; these larvae pupated on August 23 and reached the adult stage on September 7.

These two experiments, with others not mentioned here, made at different times throughout the summer, show that the duration of the post-embryonic development is about the same, approximately two months, whether the eggs be laid at the beginning of either June or July. The length of the larval stage is also the same (four weeks) in both cases. The pupal stage, however, is much longer towards the end of the summer than earlier, being respectively 14 days and 9 days. Consequently, although no experiments were conducted for the late brood, the incubation period must be shorter at the beginning of July than in early June when the temperature is still quite low on certain days.

Table VI is a résumé which gives an approximate idea of the length of each stage in the early and late broods.

TABLE VI

BIOGRAPHICAL DATES ON THE EARLY AND LATE BROODS OF 1934 IN GASPÉ PENINSULA

Early brood:	
June 3 and 4	Males enter the tree.
June 5 and 6	Females lay their first eggs.
June 24	Appearance of the first stage larvae.
July 21	Few larvae have reached the pupal stage.
July 29 and 30	Larvae which pupated on July 21 reach the adult stage.
Late brood:	
July 9	Males and females caged on a tree.
July 10	Females caged on July 9 lay their first eggs.
July 25	Eggs hatch.
August 23	Appearance of the first pupae.
September 7	Young adults.

III. Population in a Single Tree and Mortality

The number of beetles breeding in an infested tree varies directly as the area of the tree harboring *Ips perturbatus*. If the latter, instead of being the only species occupying the upper part of the trunk, is mixed with *Ips borealis* Sw. and *Dryocoetes affaber* Mannh., its number may be reduced to a minimum, sometimes less than 1,000. However, in certain cases where the weakened condition of the tree is due not to *Dendroctonus* but to *Diprion polytomum*, *Ips perturbatus* may occupy the total area of the trunk and the number of larvae reaching maturity will probably be more than 50,000. This is, however, a case peculiar to the Gaspé Peninsula, where two outbreaks, the spruce saw-fly and *Dendroctonus piceaperda*, occur simultaneously. In general the portion of the trunk infested by *Ips perturbatus* varies between 15 and 30 feet and the number of beetles reaching maturity is 10,000 to 20,000.

The most exact manner of obtaining information on the population of a tree infested by *Ips perturbatus* would be to peel carefully the whole tree under observation and make an exact count of the beetles found under the bark. It is possible, however, to obtain quite precise data by stripping the bark only on certain sections of uniform length and uniformly spaced. The latter method was the one followed for this population study.

The tree used had a total length of 66 feet and a D. B. H. of nine inches. The distribution of the different species of bark-beetles under the bark of the trunk was, from the base to the top, as follows:

Dendroctonus zone: 13 feet long; diameter at the lower part, 9 inches; diameter at the upper part, 7 inches.

Ips perturbatus zone: 32 feet long; diameter at the lower part, 7 inches; diameter at the upper part, 4 inches; average circumference, 18 inches; total superficies, 48 feet.

Ips borealis zone: 18 feet long; diameter at the lower part, 4 inches; diameter at the upper part, 1 inch, *i.e.*, 3 feet from the top.

Pityophthorus sp. zone: the last three feet.

On the portion of the trunk infested by *Ips perturbatus*, three sections, A, B and C respresenting the lower, middle and upper part of the infested portion, were cut. Their dimensions were:

Section A: 2 feet long × 20 inches circumference; cut at 9 feet from the base of *Ips perturbatus* zone, *i.e.*, at 22 feet from the D. B. H.

Section B: 1 foot long × 16 inches circumference; cut at 17 feet from the base of *Ips perturbatus* zone, *i.e.*, at 30 feet from the D. B. H.

Section C: 2 feet long × 15 inches circumference; cut at 22 feet from the base of *Ips perturbatus* zone, *i.e.*, at 35 feet from the D. B. H.

These three sections being cut, the bark was carefully removed and an exact count of the egg tunnels, egg niches, larvae, pupae, young adults, parasites, etc., was made.

Among the different methods of analyzing bark-beetle populations, the one proposed by Golovjanko and later modified by Iljinsky seems to be the most suitable. These two quantitative methods of special population studies, with many others, are very well summarized in a paper by de Gryse (6).

Using, with few modifications, the system of symbols devised by Iljinsky, the analysis of the above population study shows the following interesting facts:

A. Number of egg tunnels per square foot = 50*

M. Number of egg niches per square foot = 1225

O. Number of young adults per square foot = 502

b. Density of attack $= \frac{A}{1 \text{ (square foot)}} = 50$

d. Average number of eggs per egg tunnel $= \frac{M}{A} = 24$

c. Average number of young beetles per egg tunnel $= \frac{O}{A} = 10$

f. Percentage of mortality $= \frac{100(d - c)}{d} = 58.33$

The high percentage mortality "f" is the most striking character of all these data. This high percentage is almost entirely due to the factor "b", density of attack. Golovjanko was also of that opinion when he stated in his conclusions: "A decrease in, 'b' is followed by (i) an increase in the number of larval tunnels; (ii) *an increase in the percentage of larvae successfully completing their development . . . . .*" Iljinsky also shows conclusively that the density of attack is in itself a factor affecting the favorableness of the environment.

There are two reasons why a high density of attack of *Ips perturbatus* reduces the progeny of the families to less than half the original number: (i) The scarcity of food; in fact, it would be quite impossible for the progeny of 50 females per square foot, laying a total of 1,225 eggs, thus giving an average

** All these figures are obtained from section B only, since this is the only one where all the egg niches were counted.*

of 9 larvae to the square inch, to reach maturity in such a restricted space. Some will necessarily die by starvation. (ii) The other reason for this high percentage of mortality lies in the fact that when the density of attack is high a condition is often found in which, the egg tunnels are very near one another, almost contiguous. In such a case, what evidently happens is that when the young larvae of the egg tunnel have fed until they reach the egg tunnel they try to go through it, but the hardened dust which is deposited in the egg niches on one and sometimes both sides of the second tunnel will prevent the young larvae from crossing the second egg tunnel and cause them to die at that point by starvation.

All the data obtained from this population study and not indicated in the previous figures are summarized in Table VII. It can be seen readily that the estimates for this particular tree give a total number of 2,448 egg

TABLE VII

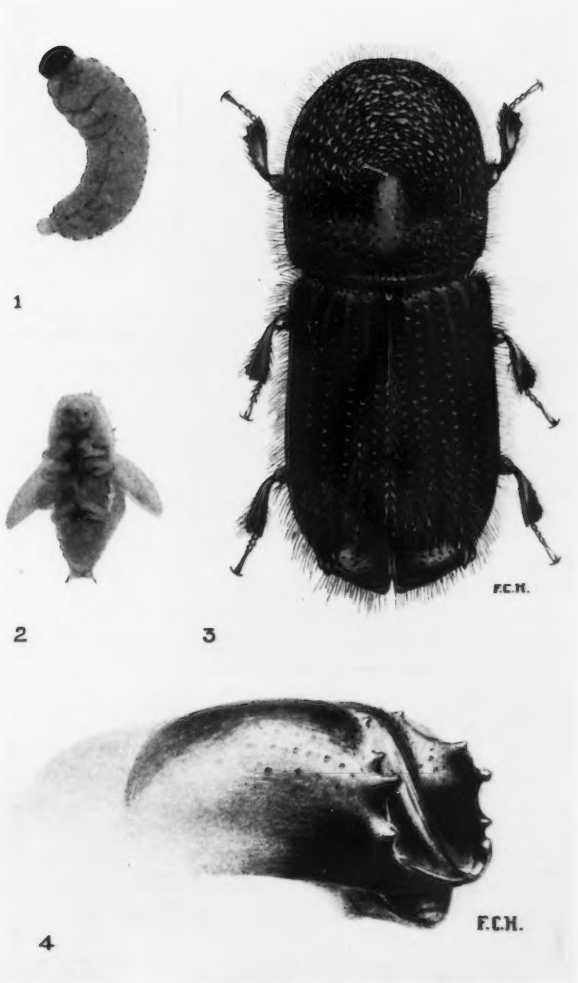
POPULATION STUDY OF *Ips perturbatus* ON WHITE SPRUCE

Section	Living adults and pupae	Dead adults and pupae	Coeloides	Egg tunnels	Egg niches	Young adults per egg tunnel	Mortality, %
A. (2 ft. × 20 in. = 3⅓ sq ft.)	1737	104	75	189		9	
Average per sq. ft.	521	31	21	57			
B. (1 ft. × 16 in. = 1⅓ sq. ft.)	669	91	21	67	1633	10	58.33
Average per sq. ft.	502	68	16	50	1225		
C. (2 ft. × 15 in. = 2½ sq. ft.)	956	53	91	115		8	
Average per sq. ft.	384	21	36	46			
Total av. per sq. ft.	469	40	25	51		9	
Total popul. of the tree	22512	1920	1200	2448	58800		

tunnels or beetle families and 58,800 eggs, out of which a total of only 22,512 larvae reached maturity. Owing to the large number of egg niches per square foot, those of Section B only were counted and from this section the figures giving the percentage of mortality were obtained.

It should be noticed that the average number of living pupae and adults is lower at the upper part of the trunk (Section C) than at the lower and middle parts, where we found the optimum conditions for *Ips perturbatus*. The thinner bark of the upper section makes the conditions less favorable for its development.

The item "dead adults and pupae" includes chiefly the pupae, since more than 50% of the progeny had reached the adult stage when the work was done. Moreover, most of the deaths were caused by *Coeloides dendroctoni* Cushman which generally kills the full-grown larvae and pupae. The number of dead pupae and adults is much larger in Section B than in the other two sections; the higher percentage of mortality in this case was caused by a white fungus surrounding the pupal cells and killing the pupae. This fungus however, was confined to only a small part of Section B.



Ips perturbatus Eichhoff.

FIG. 1. *Larva. Magnified 7 dia. (Original).* FIG. 2. *Pupa. Magnified 7 dia. (Original).* FIG. 3. *Dorsal view of the adult. Magnified 20 dia. (After Swaine (24)).* FIG. 4. *Adult, showing the declivital teeth of the elytra. Magnified 20 dia. (After Swaine, (24)).*

IV. Parasites and Predators

As a general rule parasites do not play a role of great importance in the natural control of *Ips perturbatus*. And as can be seen by Table VII of the previous section, although *Coeloides dendroctoni* Cushm. is about the only and certainly the most important parasite of *Ips perturbatus*, the percentage of mortality which may be attributed to it is not over 5.3%. On some trees these parasites seemed to be concentrated more or less in spots, and under certain pieces of bark of about 6 ×10 inches, groups of 15 to 20 cocoons were found.

Coeloides dendroctoni is also probably the most important parasite of *Dendroctonus piceaperda;* it seems, however, to prefer *Ips perturbatus*, probably because *Ips* generally breeds in the upper part of the trunk where the bark is thinner and oviposition easier. This seems to be confirmed by the fact that *Coeloides* is always more numerous on a *Dendroctonus* infested tree with rather thin bark. Thus these parasites are generally found in greater numbers on trees 9 to 12 inches in diameter than on trees 18 to 20 inches in diameter.

It should be mentioned that examples of *Coeloides dendroctoni* associated with *Ips perturbatus*, although identical with examples feeding on *Dendroctonus piceaperda*, are smaller than the latter in all stages of development (larva, pupa and adult), probably because the host is smaller.

Besides *Coeloides dendroctoni*, a few small chalcids, which had reached the adult stage when collected on August 29, were also found in the course of the population studies. These parasites were identified by Mr. G. S. Walley as belonging to the genus *Pachyceras*, family Pteromalidae. The species of this genus seem to be associated with many different bark-beetles; thus De Leon (7) records the species *Pachyceras eccoptogastri* as a primary parasite on *Dendroctonus monticolae* Hopk. The species found in the Gaspé Peninsula, however, is not common and seems to be of very little importance as a parasite of *Ips perturbatus*.

Although some predaceous insects may attack *Ips perturbatus*, none were noticed by the writer.

Among the predaceous birds, the woodpeckers, which are so effective on *Dendroctonus*, are of very small importance as control agents of *Ips perturbatus*. This is understood if we consider that the woodpeckers are chiefly active in winter when *Ips* is hidden in the ground and safe from their attacks. It is true that they could feed on the *Ips* in the summer time, but since *Ips perturbatus* is usually closely connected with *Dendroctonus piceaperda*, the woodpeckers prefer to feed on the latter species. However, since *Ips perturbatus* can breed on trees heavily defoliated by saw-fly and reach outbreak proportions even in the absence of *Dendroctonus*, the woodpeckers may in such circumstances exercise a measure of control. But actually such control, if any, must be very limited and no trace of woodpecker work has been found when the trees were cut in the fall.

Therefore it may be asserted that parasites and predators are of secondary importance as control factors of *Ips perturbatus*. The only effective check on the increase of the species is the absence of food, *i.e.*, the absence of trees

possessing the degree of weakness and dryness required to render them suitable as breeding places. Consequently, the decrease of primary outbreaks caused by *Dendroctonus piceaperda* or by *Diprion polytomum* will be the only adequate factors in ending *Ips perturbatus* outbreaks.

Acknowledgment

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